

HOME RANGES, RESOURCE SELECTION, AND
SURVIVAL OF ADULT FEMALE BLACK BEARS IN A
MIXED-OAK HABITAT TYPE IN NORTHCENTRAL
PENNSYLVANIA

By

BRANDON M. SNAVELY

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Thesis Approved:

Dr. Robert C. Lonsinger

Thesis Adviser

Dr. M. Colter Chitwood

Dr. W. Sue Fairbanks

Dr. Matthew J. Lovallo

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Abstract:

From 2019–2021, hunting seasons for American black bears (*Ursus americanus*) in Pennsylvania increased in length and changed in structure compared to prior years. Factors that influence bear harvest vulnerability during these expanded hunting seasons are unknown. Fall movement patterns of bears vary annually and may depend on fall hard mast availability. Understanding the variability in movements among bears throughout hunting seasons and their fates can inform management. We trapped and GPS-collared adult female bears in the Sproul State Forest in northcentral Pennsylvania from 2019–2021 to determine home range sizes, patterns of resource selection, and sources of mortality. We assessed the relative abundance of fall hard mast to characterize annual variability in mast availability. We evaluated temporal and spatial variation in hunter activity with road-side surveys and remote trail cameras, respectively. Beginning 1 September, we estimated fall and weekly home range size with utilization distributions through an autocorrelated kernel density estimation and evaluated the influence of predictors hypothesized to influence third-order resource selection through generalized linear mixed models. We investigated factors hypothesized to influence survival during bear hunting seasons with known-fate models. Mean fall home range size was 248.7 km² (range = 6.1–2636.1 km²). Home range size varied by year and were generally smaller during archery harvest season than other periods. Patterns of weekly resource selection indicated bears shifted their space use to areas with lower elevations and steeper slopes during hunting seasons. Bears selected for areas containing oak trees throughout the fall. Survival was lower in older age bears, higher relative mast abundance conditions, steeper slopes, and areas of greater hunter space use during the general firearms season. Survival was higher in areas of greater hunter space use during archery season. Harvest rate of adult female bears was 0.345 in 2019, 0.321 in 2020, and 0.150 in 2021, and averaged 0.272 across all three years. The probability of an adult female black bear surviving all harvest seasons each year was 0.611 (SE = 0.086, 95% CI = 0.436, 0.761). The high harvest rate and low predicted survival may lead to population reduction.

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CHAPTER I

HOME RANGES AND RESOURCE SELECTION OF ADULT FEMALE BLACK BEARS IN A MIXED-OAK HABITAT TYPE IN NORTHCENTRAL PENNSYLVANIA

INTRODUCTION

Mammals and other taxa constrain their movement patterns to distinct areas that are regularly used to meet their dietary needs, raise offspring, and breed (i.e., home ranges; Burt 1943). Understanding the biological factors influencing home ranges is crucial to elucidating aspects of space use of animals (Powell and Mitchell 2012). Space use can be assessed by the evaluation of the selection for or against resources. The patterns exhibited by animals' resource selection tendencies are a product of their survival, reproduction, and habitat quality (Boyce and McDonald 1999). Resource selection is typically assessed at four general orders, which progressively decrease in overall scale: range of a population (first-order), home range (second-order), within home range (third-order), and site-specific (fourth-order; Johnson 1980).

Home ranges of the American black bear (*Ursus americanus*) are most often annually stable and have similar local sizes that may depend on age, sex, reproductive status, food availability, and seasonality (Mitchell and Powell 2007). However, long

exploratory movements outside of home ranges occur during the fall as bears pursue sufficient food resources to meet the needs of hyperphagia (Garshelis and Pelton 1981). In Pennsylvania, the mean annual home range sizes of adult male bears and adult female bears were $\sim 173 \text{ km}^2$ and $\sim 41 \text{ km}^2$, respectively (Alt et al. 1980). Within home range (i.e., third-order) resource selection patterns may vary among systems or over time. Previous bear studies have evaluated resource selection as a function of covariates including landcover, season, year, and distances to natural and anthropogenic features (Joshi et al. 1995, Mace et al. 1996, Stratman et al. 2001, Nielsen et al. 2002, Carter et al. 2010, Hiller et al. 2015, Tri et al. 2016). In Pennsylvania, bears did not alter their patterns of resource selection based upon harvest seasons or hunting access (Ahrestani et al. 2020). Regardless of sex, bears selected for forested, herbaceous, and riparian landcovers, and forested slopes (Tri et al. 2016). However, bears avoided human-developed habitat types (Tri et al. 2016), and evidence existed to suggest that bears perceived anthropogenic landscape features as risky (Ditmer et al. 2018).

Black bears occupy 45–60% of their historical range in the United States with most of Pennsylvania within their primary range; far southeast portions of Pennsylvania and areas along the Pennsylvania-Ohio border are not part of their primary range (Scheick and McCown 2014). In Pennsylvania, the population was $\sim 3,500$ bears in the 1970s and was restricted to the northcentral and northeast regions of the state. From 1980–2001, the bear population in Pennsylvania increased in abundance to $\sim 15,000$ bears and increased in distribution to $>75\%$ of the state. From 2002–2019, the bear population in Pennsylvania continued to increase and was estimated to be $>20,000$ bears in 2019 (Ternent 2006, Carrollo 2021).

From 2019–2021, the Pennsylvania Game Commission (PGC) increased the length of bear harvest seasons and began harvest seasons earlier than in previous years to increase bear hunting opportunity and stabilize the abundance and distribution of bears. Human induced mortality (especially hunting) is commonly the primary source of bear mortality (Kasworm and Thier 1994, Larivière 2001). Hunting intensity and other human disturbances on the landscape may impact space use of large mammals due to perceived risks (Millsbaugh et al. 2000, Frid and Dill 2002). Because harvest seasons have changed, the perceived risks of predation of bears may have changed and may lead to temporal variation in space use patterns during periods of harvest and non-harvest. Therefore, understanding the dynamic patterns of bear home range size and shifts in resource selection within home ranges during harvest can inform management to achieve bear population goals.

The probability that an animal uses certain locations and the resources therein, as compared to what is available, can be used to assess patterns of resource selection. Resource selection functions provide a method to better understand the factors driving animal use of resources at varying scales (Manly et al. 2002). Here, we evaluated changes in home range sizes and assessed patterns of third–order resource selection of black bears in Pennsylvania throughout the fall. Unlike previous analyses on home range size and resource selection, we performed analyses at a finer temporal resolution (i.e., weekly) to identify patterns of space use that may go undetected at a coarser scale. Using location data from GPS-collared bears, we evaluated the following questions: (i) do weekly home range sizes vary throughout the fall; and (ii) how do weekly patterns of third-order resource selection for natural and anthropogenic habitat variables vary throughout the

fall? Bears in rural areas may alter their behavior based on human activity (Zeller et al. 2019), and human activity may increase in rural areas during hunting seasons. Thus, we predicted that home range size would increase during bear hunting seasons due to a response to the perceived risk of harvest (Laundré et al. 2010) and that home range size would exhibit a great degree of variability among individuals. Additionally, based on patterns of black bear avoidance of anthropogenic landscape features (Brody and Pelton 1989, Kasworm and Manly 1990), we predicted that bears would select against anthropogenic features and these patterns of resource selection would be especially prominent during periods of bear harvest. We predicted that bears would select for steeper slopes and lower elevations (more remote regions) during harvest to avoid hunters (Tri et al. 2016) and that bears would select for oak stands, which are important for foraging on mast (Pelton 1989).

METHODS

Study area

Our study occurred in an approximately 308-km² area in northcentral Pennsylvania (Figure 1.1). The study area encompassed 240-km² that has been used since 2002 for annual baseline monitoring of black bear reproductive parameters (Ternent 2018). The study area was entirely within the Sproul State Forest south of Renovo, Pennsylvania, and encompassed portions of Clinton and Centre counties in the west branch of the Susquehanna River drainage. The study area was bounded by the West Branch of the Susquehanna River to the north, State Route 120 to the east, State Route 144 to the west, and the southern boundary of the Sproul State Forest. The entirety of the study area was public land and was accessible to recreation (e.g., hunting). Some of the

highest bear harvest densities and overall bear harvest in Pennsylvania occurred within the study area (Ternent 2019).

The study area was representative of northcentral Pennsylvania's expansive forested habitat and was approximately 97% forested. The study area was predominantly mixed-oak hardwood forest. Forests of various successional stages were interspersed throughout the study area. Younger regenerating forests throughout the study area resulted from logging operations and infrequent wildfires. The primary land uses included timber management, multiple-use recreation, and natural gas extraction. Small openings associated with natural gas extraction (~2 ha) and hunting camps (~0.1–8 ha, usually small buildings of simple construction) were interspersed within the study area. Dominant tree species included red oak (*Quercus rubra*), white oak (*Q. alba*), chestnut oak (*Q. montana*), and red maple (*Acer rubrum*). Understories species consisted primarily of mountain laurel (*Kalmia latifolia*), great rhododendron (*Rhododendron maximum*), Japanese stiltgrass (*Microstegium vimineum*), sweet fern (*Comptonia peregrina*), and lowbush blueberry (*Vaccinium pallidum*). Potential mammalian prey species for the American black bear in the study area included white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus canadensis*), whereas potential competitors (especially for hard mast in the fall) included white-tailed deer, elk, wild turkey (*Meleagris gallopavo*), and eastern gray squirrel (*Sciurus carolinensis*).

The study area lies on the southern edge of the Appalachian Plateau Province, adjacent to the Ridge and Valley Province, and has elevations between 305–760 m. Soils along the narrow ridges and steep slopes were shallow and low in fertility (NRCS 2019). From 1981–2021, the study area experienced average annual high temperatures of 16.1

°C, average annual low temperatures of 3.8 °C, average annual precipitation of 100.9 cm, and average annual snowfall of 81.3 cm. Average temperatures in Renovo, PA were 9 °C in spring (March-May), 21 °C in summer (June-August), 11 °C in fall (September-November), and -2 °C in winter (December-February; US Climate Data; Renovo, PA 2020).

Capture and tracking

We captured bears during the summers of 2019, 2020, and 2021 in conjunction with the PGC's long-term reproductive study on the Sproul State Forest (Ternent 2018). We divided the study area into 5 regions and sequentially trapped each region for 8 consecutive days from late May through August annually. In accordance with historical trapping locations for the reproductive study, we deployed barrel-style traps at an approximate density of 1 trap/4 km². We baited traps with waste pastries (Gould et al. 2021) and checked them daily.

During summer captures in 2019, we immobilized captured bears with either 1.0 ml/45.5 kg NalMed-A (also known as NAM; 40 mg/ml nalbuphine hydrochloride, 10 mg/ml azaperone tartrate, and 10 mg/ml medetomidine hydrochloride), 1.0 ml/45.5 kg BAM (50 mg/ml butophanol hydrochloride, 50 mg/ml azaperone tartrate, and 20 mg/ml medetomidine hydrochloride), or a 2:0.8 mixture of ketamine hydrochloride (4.4 mg/kg) and xylazine hydrochloride (1.8 mg/kg) delivered intramuscularly by CO²-propelled darts. During summer captures in 2020 and 2021, we exclusively immobilized captured bears with 1.0 ml/45.5 kg NalMed-A delivered intramuscularly by CO²-propelled darts (Wolfe et al. 2008, Wolfe et al. 2016, Williamson et al. 2018). We tagged each bear in both ears with uniquely numbered metal tags (style 56-L, size 36.5 × 9.5 mm; Hasco Tag

Company, Dayton, Kentucky). We tattooed the lower of the two ear tag numbers on the inside of the upper lip for bears ≥ 1 year old. We replaced ear tags that were missing from recaptured bears. We fitted an Iridium GPS satellite collar (Vertex Lite with 2D battery, Vectronics, Germany) on each female bears weighing ≥ 40 kg, including the replacement of any very-high-frequency (VHF) collars (Advanced Telemetry Systems, Isanti, Minnesota) that were on previously captured female bears. For each captured bear, we recorded the date, capture location, ambient air temperature (via handheld Kestrel weather station), vital rate measurements (i.e., temperature, heart rate, and respiration rate), sex, weight, and standard physical measurements (e.g., head, paw, and total body size measurements). We also collected an upper first premolar for age determination from adult bears of unknown age (Harshyne et al. 1998). For female bears, we noted vulva swelling, teat condition, evidence of lactation, and sighting of offspring to determine reproductive status (i.e., with cubs, with yearlings, or solitary). We used atipamezole HCL (5 mg/mg) and naltrexone HCL (1.3 mg/mg) to reverse immobilization of captured bears anesthetized with BAM and NalMed-A, and we used yohimbine hydrochloride (0.15 mg/kg) to reverse immobilization of bears anesthetized with the Ketamine/Xylazine mixture. We remained at the trap site until ambulatory recovery was observed. In accordance with winter black bear den monitoring by the PGC, project personnel or PGC staff visited dens of radio-collared bears in February or March of 2020 and 2021 and recovered location data not transmitted by satellite connections, adjusted fit of radio-collars, and replaced leather breakaway splices. For captured bears during den visits, project personnel or PGC staff immobilized bears with a 2:0.8 mixture of ketamine hydrochloride (4.4 mg/kg) and xylazine hydrochloride (1.8 mg/kg) that was delivered

intramuscularly by CO²-propelled darts. Immobilization was not reversed during den visits and we did not remain at the capture site until ambulatory recovery was observed. All capture and handling procedures were in accordance with guidelines endorsed by the American Society of Mammalogists (Sikes et al. 2016) and sanctioned by the Institutional Animal Care and Use Committees for South Dakota State University (Protocol 2002-005A) and Oklahoma State University (Protocol IACUC-21-19).

Radio-collars were programmed to attempt a GPS-location fix every 2.25 hours. We retrieved location and activity data from collars using satellite connections (via GPS Plus X and Inventa; Vectronics, Germany) or by physical download when the collar was recovered (e.g., when a collared black bear was harvested or recaptured). We monitored radio-collared black bears daily using a remote satellite connection, and any stationary collar that indicated a mortality event (i.e., inactive for ≥ 8 hours) was investigated by project personnel or PGC staff to determine the cause of the mortality event. During hunting seasons, all harvested black bears statewide were examined by the PGC at check stations and any ear tags were noted.

Home range analyses

We evaluated weekly and fall home range sizes for each collared bear over the period from 1 September until den entry or mortality each year. We determined den entry by identifying clusters of locations in which an individual spent greater than five days and remained at over winter. We determined time of mortality through PGC harvest records and by determining the last collar location without mortality suspected. Only individuals with ≥ 30 locations were analyzed for any given period (e.g., week). We used the R package ctmweb in the program R version 4.2.0 (Calabrese et al. 2021, R Core

Team 2022) and autocorrelated kernel density estimation (AKDE) to produce 95% fall home range estimates, and 95% and 50% weekly home range estimates. All locations that were available for each bear within each fall and weekly period were used for analyses. Movement models via variogram analysis for each home range estimate were automated to determine the structure of autocorrelation of the data and the most-supported movement model was selected based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002, Calabrese et al. 2021). We calculated mean AKDE estimates and standard errors for each period assessed. We assessed home ranges at varying levels because we were interested in both traditional home range estimates (95% estimates) and core home range areas (50% estimates; i.e., core-use areas), especially because the periphery of 95% home range estimates may include areas that were never or rarely used (Powell 2000). Additionally, some covariates used to assess resource selection were only available for public lands; therefore, using 50% home range estimates mitigated data loss from data thinning procedures (see Resource selection analyses).

Resource selection analyses

We used weekly 50% AKDE home range estimates to assess variation in resource selection by bears over the period from 1 September through den entry or mortality events. All used locations within the 50% AKDE home range estimates were included in analyses. We set the number of available points equal to 10 times the number of used points (Ahrestani et al. 2020) and randomly generated available points with the R package *amt* for animal movement tools (Signer et al. 2019). To assess resource selection, we extracted values of eight covariates associated with topography (i.e., elevation and slope), land cover (i.e., canopy height, oak stands, and distance to rivers or

streams), and anthropogenic features (i.e., distance to state forest camps, distance to primary roads, and distance to secondary or gated roads; Table 1.1). Distance to state forest camps, distance to primary roads, and distance to secondary or gated roads may influence bear space use if they perceive risk from roadways or avoid anthropogenic features (Tri et al. 2016, Ditmer et al 2018). Additionally, elevation may be important as bears may select for the most remote areas of the study area, which generally occurred at the lowest elevations near riparian areas and farthest away from vehicle traffic. Bears have selected for forested slopes and riparian areas during hunting seasons (Tri et al. 2016). However, in our study area, these riparian areas generally contained hiking trails used by hikers and hunters. Consequently, landscape features characterized by low elevation with steep slopes in our study area (e.g., narrow draws commonly associated with riparian areas) may have the potential to concentrate human odors that bears may adeptly recognize due to pronounced olfactory senses and could cause selection against these areas. Canopy height may explain potential differences in forest structure, which may impede sight and movement in some areas or facilitate foraging in others. For example, hard mast producing oak stands are typically the most influential for supplying energy sources for bears (Inman and Pelton 2002).

We obtained layers for elevation (m), slope (degrees), canopy height (m), primary roads, and streams and rivers from 2020 LANDFIRE (<https://landfire.cr.usgs.gov/>). We obtained shapefiles (2021) for secondary or gated roads, state forest camps, and forest stand types from the Pennsylvania Department of Conservation and Natural Resources. We reclassified the canopy height raster to create a continuous covariate, and we reclassified forest stand types as a binary covariate for oak stands (1) and non-oak stands

(0). For used and available points, we extracted values for elevation, slope, canopy height, and stand type with the Extract Multi Values to Points tool in ArcMap 10.8.1 (ESRI, Redlands, CA). We used the Near tool in ArcMap to calculate the distance (m) from both used and available points to rivers or streams, primary roads, secondary or gated roads, and state forest camps.

We performed third-order resource selection analyses to determine the selection of resources within each individual's home range by comparing the use of resource features relative to their availability (Johnson 1980, Manly et al. 2002). We standardized continuous covariates (i.e., elevation, slope, canopy height, distance to rivers or streams, distance to state forest camps, distance to primary roads, and distance to secondary or gated roads). We assessed pairwise correlations among predictors by using the `cor` command in R via the Pearson method. We considered any pair of covariates with $|r| > 0.7$ as being highly correlated (Nielsen et al. 2002). When two covariates were highly correlated, we retained the covariate that was hypothesized to have a greater influence on patterns of resource selection for subsequent analyses. To assess third-order resource selection, we developed 27 *a priori* models reflecting hypotheses about factors driving female black bear resource selection (Appendix A). We used the R package `lme4` (Bates 2010) to assess resource selection with generalized linear mixed effects models (GLMMs) for our model set. A unique bear identifier was included as a random effect in each model to account for variation in selection of resources among individuals (Gillies et al. 2006). We assessed resource selection by comparing used (1) and available (0) points that were coded as a binary response. For model selection, we used Akaike's

Information Criterion corrected for small sample sizes (AICc; Akaike 1973, Burnham and Anderson 2002).

We subsequently conducted two post-hoc analyses. We compared the most-parsimonious model from each week to a model with year as an additional random effect to account for temporal heterogeneity not accounted for by our covariates. Next, we compared the most-parsimonious model from the year analysis to models that included a binary covariate indicating if an individual was harvested (1) or not (0) as a fixed effect. Following consideration of post-hoc comparison of models including year and harvest, we used the most-parsimonious model to assess resource selection for a given week. We subsequently generated predictive maps of high-scaled space use (>0.6) from the most-parsimonious models from each week and combined the resulting shapefiles into periods (i.e., pre-hunting season during weeks 1–7, muzzleloader/archery/special firearms season during weeks 8–10, middle non-hunting season during weeks 11–12, and rifle season during week 13) by taking the mean estimated use across weeks during those periods.

RESULTS

Capture and Trapping

We deployed traps in the same locations each year from 29 May–20 August 2019, 28 May–18 August 2020, and 2 June–27 July 2021. Over the three years, 46.4% of captured bears were adult females, whereas 30.1% were adult males, 12.0% were juvenile females, and 11.4% were juvenile males (Table 1.2). Trapping efficiency, the total number of bears captured and processed, and adult females captured declined from 2019–2021 (Table 1.2). We deployed 29 new collars during 2019 trapping, and one bear was previously trapped and collared in 2018 by PGC staff with the same collar model,

resulting in 30 collared females for our analyses. During 2020 winter den checks, we deployed three collars on adult female bears that were previously outfitted with VHF collars. During 2020 trapping, we deployed 11 new collars, which resulted in 29 collared females for our analyses. During 2021 winter den checks, we deployed four collars on adult female bears that were previously outfitted with VHF collars. During 2021 trapping, we deployed four new collars on adult female bears, which resulted in 20 collared females for our analyses. However, due to vehicle collisions and collar malfunctions we were able to use 29 collared females in 2019, 28 collared females in 2020, and 16 collared females in 2021 for analyses.

Though we collared 45 total adult female bears, the annual reduction in trap success and captures, paired with loss of collared animals due to vehicle collisions, collar malfunctions and harvest resulted in a decline in the number of adult female bears outfitted with GPS collars each year. The quantity of GPS locations, number of GPS collared bears, and number of harvested individuals decreased over the course of the study (Table 1.3). A lower proportion of collared bears was harvested during archery seasons than other harvest seasons, despite the archery season having the longest duration (Table 1.3). Additionally, we obtained fewer GPS locations later in the fall due to harvest and den entrance, both of which reduced the number of active collared bears (Table 1.3).

Home range analyses

The average home range size during the fall across all three years was 248.7 km² (range = 6.1–2636.1 km²), and estimates were lower in 2021 than in 2019 or 2020 (Figure 1.2). Whether considering the entire fall season estimates (Figure 1.2) or weekly estimates (Figure 1.3), 95% home range sizes were generally largest in 2020 and smallest

in 2021. On average, home range estimates of harvested bears were generally larger than those of non-harvested bears across all weeks (Figure 1.4). Additionally, home ranges were generally smaller during the weeks where the archery harvest season occurred than all other weeks (Figure 1.3, Figure 1.5). Estimated 50% weekly home ranges exhibited similar patterns to 95% weekly home ranges across weeks and year (Figure 1.3, Figure 1.5). The number of individuals included in home range estimation declined with time as animals were harvested, entered a den, or experienced a collar malfunction.

Resource selection analyses

We assessed weekly third-order resource selection for female black bears during weeks 1–15, where week 1 started on 1 September each year. We were unable to assess resource selection during weeks 16–17 due to sample sizes of ≤ 3 individuals during those weeks. The most-parsimonious model of third-order resource selection in 12 of the 15 weeks included additive effects of slope, elevation, cover height, oak stand, and distance to streams and rivers, paved road, secondary/gated roads, and camps (Table 1.4, Figure 1.6). The most-parsimonious model for week 6 included only distance to stream and oak stand, whereas the most-parsimonious model for week 9 included only slope and elevation (Table 1.4). The most-parsimonious model for week 14 included slope, elevation, distance to stream, cover height, and oak stand. The number of bears used for analyses and their used points decreased throughout the duration of the study (Table 1.3). The addition of harvest status to the weekly top model did not improve model fit for any week. The addition of the random effect of year only improved model fit (relative to the model without the year effect) in week 15 ($\Delta AIC = 0.62$). Consequently, to maintain

consistency among weeks, we decided to assess the beta coefficients for models without a year effect for all weeks (including week 15).

Slope and elevation were in the most-parsimonious model during each week where harvest seasons occurred (Figure 1.7). Bears generally selected for steeper slopes outside of bear harvest seasons. However, the direction of effect of slope changed from negative to positive from weeks 6–12, indicating bears were initially selecting for areas with less slope but then switched to selecting for steeper slopes. Bears generally selected for higher elevations outside of bear harvest seasons and generally lower elevations during harvest seasons. Bears generally selected for oak stands throughout the fall. Bears selected for areas with lower tree heights outside of and during harvest seasons; however, bears selected for areas with greater tree heights in the first week of bear harvest. Bears selected for areas farther from streams and rivers outside of bear harvest seasons; however, during weeks 8–10, bears changed their selection by initially selecting areas farther from streams and rivers and then switching to selecting areas closer to streams and rivers. Bears initially selected for areas farther from both paved and secondary/gated roads prior to harvest seasons, then selected for areas closer to all roads in weeks 8–10, and finally selected for areas farther from all roads from weeks 11–15. Distance to camp was included in the most-parsimonious model for 12 weeks; however, the confidence intervals for this covariate routinely overlapped zero. During the general firearms season (week 13), we observed the strongest selection by bears for areas closer to camps. There was increased uncertainty for beta coefficients (β) as sample size decreased (particularly in weeks 14 and 15; Figure 1.7). During the pre-hunt weeks, space use was uniformly distributed across the study area. Then, during the weeks that contained muzzleloader,

archery, and special firearms harvest seasons, we observed a shift in space use towards lower elevation and more remote regions of the study area. Next, during both the middle non-hunting season and firearms harvest season, bear space use was much more sporadically dispersed, leading to few areas of high use (Figure 1.8).

DISCUSSION

Home ranges

Defining time intervals for analyzing home ranges is important to understanding the cognitive map of an animal (Botani and Powell 2012). Assessing patterns of home range sizes at a finer temporal resolution than previous studies allowed us to evaluate nuances in patterns of space use that may have otherwise gone undetected at coarser temporal scales. Finer temporal resolution helped us to better understand when shifts in space use occurred. Home range sizes may depend on seasonality of food production and mortality risk (McNab 1963, McLoughlin and Ferguson 2000). The home ranges of many female mammal species, including bears, may be greatly affected by the variability of food abundance on the landscape (Powell et al. 1997). The home range sizes of black bears vary greatly across North America (Larivière 2001) and are typically larger during fall than summer (Moyer et al. 2007). Adult female bears in similar deciduous forest systems have been documented as having fall home range sizes of $\sim 4 \text{ km}^2$ (Arkansas; Smith and Pelton 1990), $\sim 15 \text{ km}^2$ (Great Smoky Mountain National Park; Garshelis and Pelton 1981), and $\sim 21 \text{ km}^2$ (Maryland; Jones et al. 2015). During previous research in Pennsylvania, monthly fall home range estimates of adult female black bears were as high as $\sim 50 \text{ km}^2$ for both females with cubs and pregnant females (Alt et al. 1980). The average fall home range estimate that we observed in our population of adult female

bears was 248.73 km², which is a substantially larger estimate than what has often been recorded as fall home range estimates of bears of either sex. These larger estimates may be attributed to two things: retaining exploratory trips in our home range estimation and using AKDEs to estimate home range sizes. We retained exploratory trips because they were important in capturing all fall movement patterns, not just when bears remained in “core” areas. Although AKDEs have been shown to produce home range estimates that are magnitudes larger than more conventional home range estimators (Morato et al. 2016), we used AKDEs because our data were temporally auto-correlated and conventional home range estimators tend to underestimate home range sizes (Fleming et al. 2015). Additionally, AKDEs allowed us to estimate home range sizes and compare individuals with different movement patterns without requiring data thinning (Fleming and Calabrese 2017). Our estimates from 2021 aligned more closely with previous estimates for female bears in similar landcover; however, we did not observe long exploratory movements by bears in 2021.

Home range shifts in mammals occur seasonally and may be driven by the distribution of food resources (Szemethy et al. 2003, Moore et al. 2018). Mast and other fall food sources can influence the magnitude of home range shifts in bears (Garshelis and Pelton 1981). Bears may change their foraging behavior prior to entering winter dens, and pregnant females enter dens earlier than females with offspring or males (Powell et al. 1997). Previous research in Pennsylvania indicated that home range sizes decreased closer to den entrance events (Alt et al. 1980). Our results indicated that home range estimates tended to be smallest during late October–early November, which aligned with the archery harvest seasons. Bears in our study generally began entering dens in

week 8 (mid to late October). The timing of den entrance and small home range estimates may have indicated that bears shifted their patterns of home range size prior to entering winter dens. Additionally, small home range estimates may be in part due to low amounts of hunters on the landscape during this period, potentially resulting in reduced effect of humans on bear movements (Larivière et al. 1994). However, bears in our study showed a great degree of variability in weekly home range size later into the fall. Greater food abundance can lead to smaller home range sizes, while lower food abundance may require more movement and therefore lead to larger home range sizes (Larivière 2001). In 2021, our home range size estimates were lowest and showed the least degree of variability among the three years of the study; however, the lowest food abundance metrics (hard mast abundance) were documented on our study area during the same time period (Chapter II). Low food abundance with small home range estimates is counterintuitive to what may often occur with fall home range patterns in bears and may indicate that other factors (e.g., hunting intensity) may be affecting home range size shifts in our study system.

Patterns of resource selection

Selection of habitat and food resources are often points of emphasis for resource selection studies (Manly et al. 2002). Black bears have been documented selecting for riparian areas, steeper slopes, and higher elevations (Tri et al. 2016, Lustig et al. 2021). Forest composition and hard mast therein are important factors that may influence bear movements and home range size during the fall (Garshelis and Pelton 1981). Additionally, patterns of resource selection of black bears may be a response to vegetative food abundance and population densities (Duquette et al. 2017). Assessing

patterns of resource selection at a finer temporal resolution allowed us to observe when shifts in selection occurred. Our results indicated oak stands were consistently selected throughout the fall, which was likely due to the importance of mast, a dominant food source for bears in the fall in our study area. We observed a change in selection for some covariates during weeks 7–8 (i.e., the week prior to harvest and the first week of harvest season). Hunter activity may be greater during weeks prior to harvest season than weeks after harvest seasons (Root et al. 1988), which may be due to scouting activities. The patterns of selection then moved closer to pre-harvest metrics after these weeks. Evidence of these patterns exist for slope, tree height, and elevation, as bears moved away from lower slopes, forest stands with greater canopy heights, and lower elevation during weeks 7–8 and then to steeper slopes, lower canopy heights, and higher elevation, respectively. Shifts in resource selection during periods just before and at the start of harvest could be a consequence of greater human activity during these periods compared to later in the harvest season, whereby an increase of humans on the landscape has a meaningful effect on patterns of bear resource selection. These shifts in selection patterns could potentially be explained by bears vacating home ranges due to hunter presence (Verdade 1996).

Anthropogenic activities can impact movement patterns for wildlife (Riotte-Lambert and Matthiopoulos 2020). Anthropogenic landscape features such as roads and trails have been documented to influence space use by bears (Kasworm and Manly 1990). Black bears have shown patterns of avoidance to roads in regions where bear harvest occurred (Brody and Pelton 1989). Bears in our study selected for areas closer to roads during weeks 8–10 (when bear harvest seasons occurred). Selection of areas closer to roads is contrary to both our prediction of bears avoiding anthropogenic landscape

features and patterns of selection previously documented in bears. These patterns may be a result of bears shifting space use to different areas in their home ranges during initial periods of time when human densities may have increased due to hunting. Alternatively, predictive mapping of high-scaled space use during this same period revealed that bears were more likely to be present in the most remote areas of our study area (which were generally away from hunting access locations). Although bears selected for areas closer to roads in their home ranges during this period, bears were still most likely to use areas that were less anthropogenically disturbed in the most remote regions of the study area.

Management implications

Shifts in patterns of home range sizes and resource selection may influence survival, food resource acquisition, and subsequent reproduction. Because patterns of resource selection regarding slope and elevation were important throughout all harvest seasons, bears may be using terrain characteristics to avoid human disturbance and ultimately avoid harvest mortality. Hunter densities and hunting pressure may influence shifts to resource selection as predicted bear use moved to remote areas during the first three weeks of harvest seasons. There is evidence that increased human presence on the landscape may at first alter bear resource selection patterns; therefore, if bears are moving to areas with suboptimal food resources to mitigate risks, decreases in food availability or nutritional quality (and potentially increased competition among bears) may lead to secondary effects on fitness, such as reduced short-term or long-term survival or decreased reproductive capacity. Manipulating the number and availability of remote areas may be influential to attaining certain population objectives, as bears may be shifting resource use due to hunting pressure. In our study system, restricting vehicle

access to secondary roads (e.g., closing gates) could increase the quantity of remote areas, which may mitigate negative effects of shifting patterns of resource selection.

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TABLES

Table 1.1. Covariates considered for resource selection functions used to assess patterns of space use for adult female black bears (*Ursus americanus*) in the Sproul State Forest in northcentral Pennsylvania during fall (2019–2021). Positive (+) and negative (-) predictions indicated covariates were expected to have a positive or negative respective association with space use.

Category	Covariate	Prediction (time)	Prediction (harvest seasons)	Unit
Topography	Elevation ¹		-	m
	Slope ¹		+	
Land Cover	Distance to rivers or streams ¹		+	m
	Categorical stand type ²			
	Oak stand	+		
	Non-oak stand	-		
Anthropogenic features	Tree height ¹		-	m
	Distance to camp ²		+	m
	Distance to primary road ¹		+	m
	Distance to secondary/gated road ²		+	m

¹ From 2020 Landfire

² From the Pennsylvania Department of Conservation and Natural Resources

Table 1.2. Results of black bear (*Ursus americanus*) trapping, including trapping effort (Trap Nights), capture events (number of traps triggered with a bear capture), number unique bears captured (Bears Captured) and processed (Bears Processed), trapping efficiency (Trap Success), and the number of unique bears captured by age-class and sex from 2019–2021 on the Sproul State Forest, PA.

Trapping Results	2019	2020	2021
Trap Nights	413	400	382
Capture Events	109	80	55
Bears Captured	70	57	39
Bears Processed	68	37	26
Trap Success	26.4%	20.0%	14.4%
Adult Females	34	26	17
Adult Males	22	14	14
Juvenile Females	7	8	5
Juvenile Males	7	9	3

Table 1.3. Number of GPS-collared adult female black bears harvested and summary of GPS-collar data for bears during 2019–2021 harvest seasons in the Sproul State Forest, PA.

Year	Harvest Season	Dates	Harvested	Bears	Fixes
2019					
	Muzzleloader	19 Oct–26 Oct	4	29	2,175
	Archery	28 Oct–9 Nov	3	25	3,328
	General Firearms	23 Nov–27 Nov	3	22	924
	Total		11^A		6,427
2020					
	Muzzleloader/Archery	17 Oct–24 Oct	7	28 ^B	2,090
	Archery	25 Oct–7 Nov	1	21	1,568
	General Firearms	21 Nov–24 Nov	1	20	853
	Total		9		4,511
2021					
	Muzzleloader/Archery	16 Oct–23 Oct	1	16 ^C	1,120
	Archery	24 Oct–6 Nov	0	15	1,941
	General Firearms	20 Nov–23 Nov	2	13	554
	Total		3		3,615

^AOne bear was killed in September 2019 by a vehicle collision

^BGPS collars on 1 of 29 bears stopped transmitting data prior to the start of bear harvest

^CGPS collars on 4 of 20 bears stopped transmitting data prior to the start of bear harvest

Table 1.4 Weekly summary of the number of adult female GPS-collared bears, used points, and most-parsimonious model from resource selection analyses during 2019–2021 in the Sproul State Forest, PA.

Week	Number of		Model
	Bears	Used Points	
1	35	2480	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
2	37	2470	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
3	38	2588	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
4	37	25440	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
5	34	2385	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
6	36	2534	Oak + DistStream
7	36	2477	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
8	32	2265	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
9	27	1910	Slope + Elev
10	27	1805	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
11	24	1547	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
12	20	1141	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
13	12	740	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads
14	7	358	Slope + Elev + Oak + TreeHeight + DistStreams
15	4	269	Slope + Elev + Oak + TreeHeight + DistStreams + DistCamps + DistPavedRoad + DistSecondaryRoads

Notes: Slope = slope (degrees); Elev = elevation (m); Oak = oak stand (1) or not (0); TreeHeight = Tree height (m); DistStreams = distance to streams or rivers (m); DistCamps = distance to state-leased hunting camps (m); DistPavedRoad = distance to primary (paved) roads (m); DistSecondaryRoads = distance to secondary or gated roads (m).

FIGURES

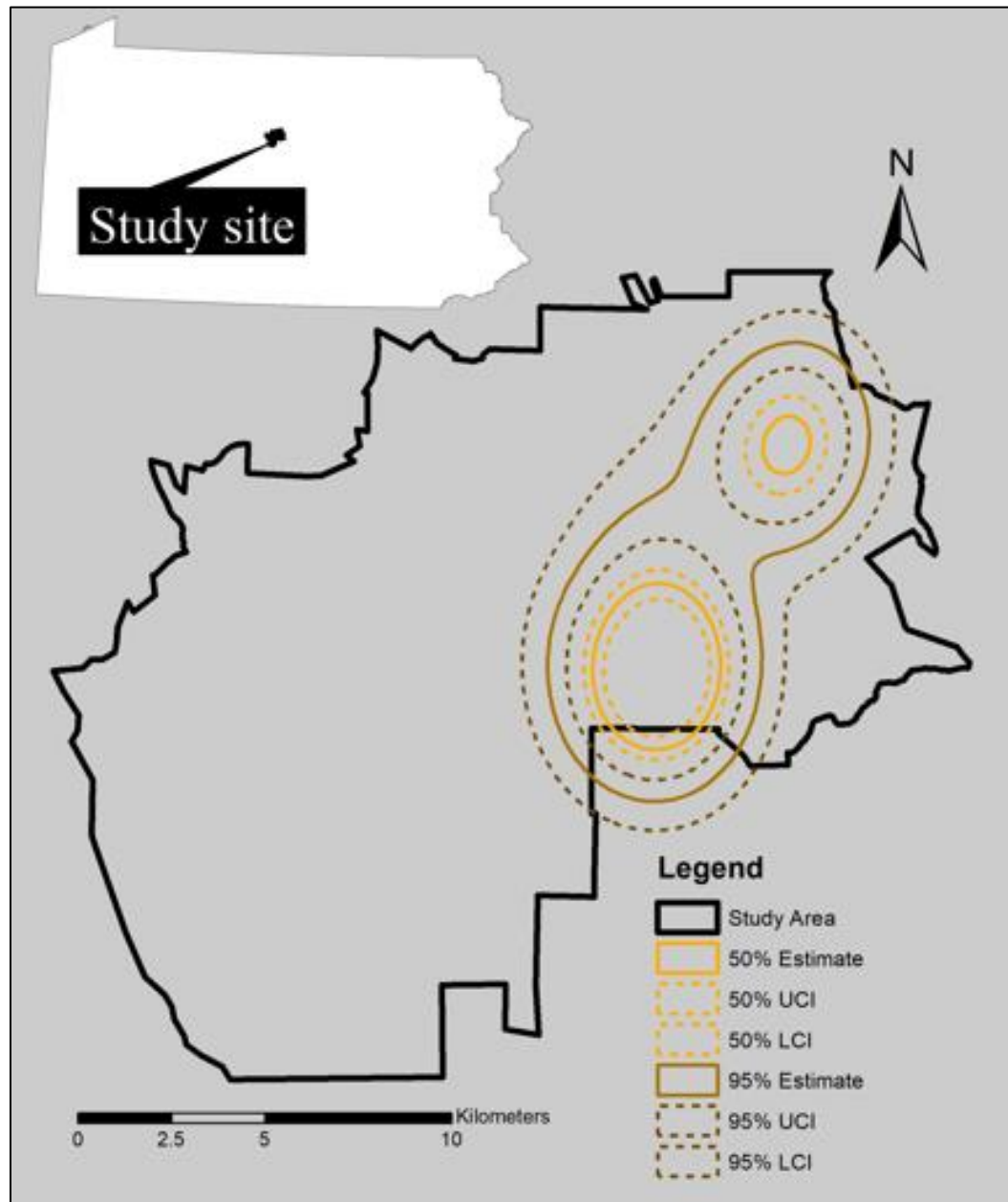


Figure 1.1. Location of the American black bear (*Ursus americanus*) study area and an example of a bear home range estimated using autocorrelated kernel density estimation (AKDE; 50% and 95%) of an adult female black bear in the Sproul State Forest in northcentral Pennsylvania.

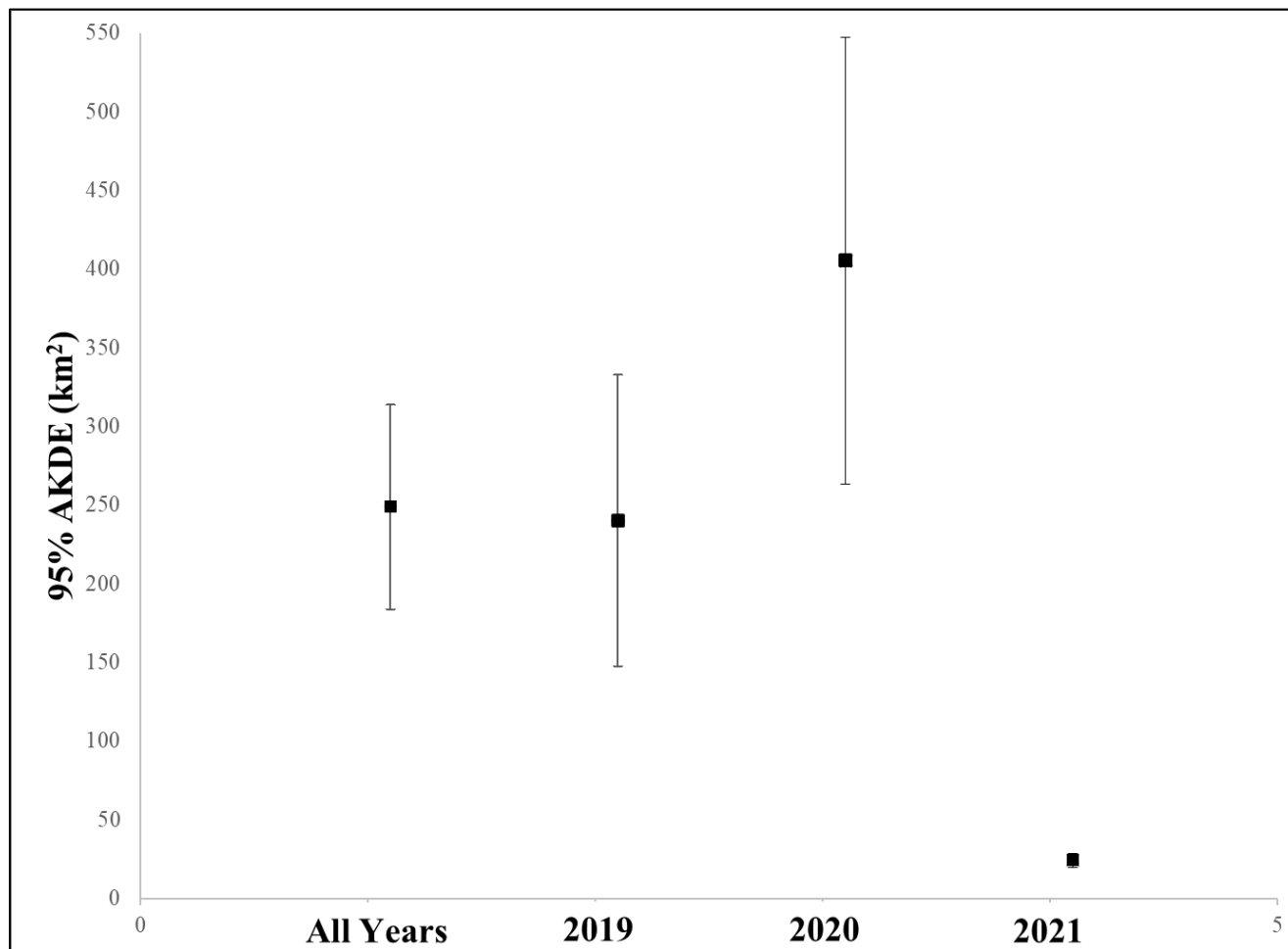


Figure 1.2. Mean 95% home ranges estimates using autocorrelated kernel density estimation (AKDEs) +/- 1 SE for adult female black bears beginning 1 September through den entry or harvest from 2019–2021 in the Sproul State Forest, PA.

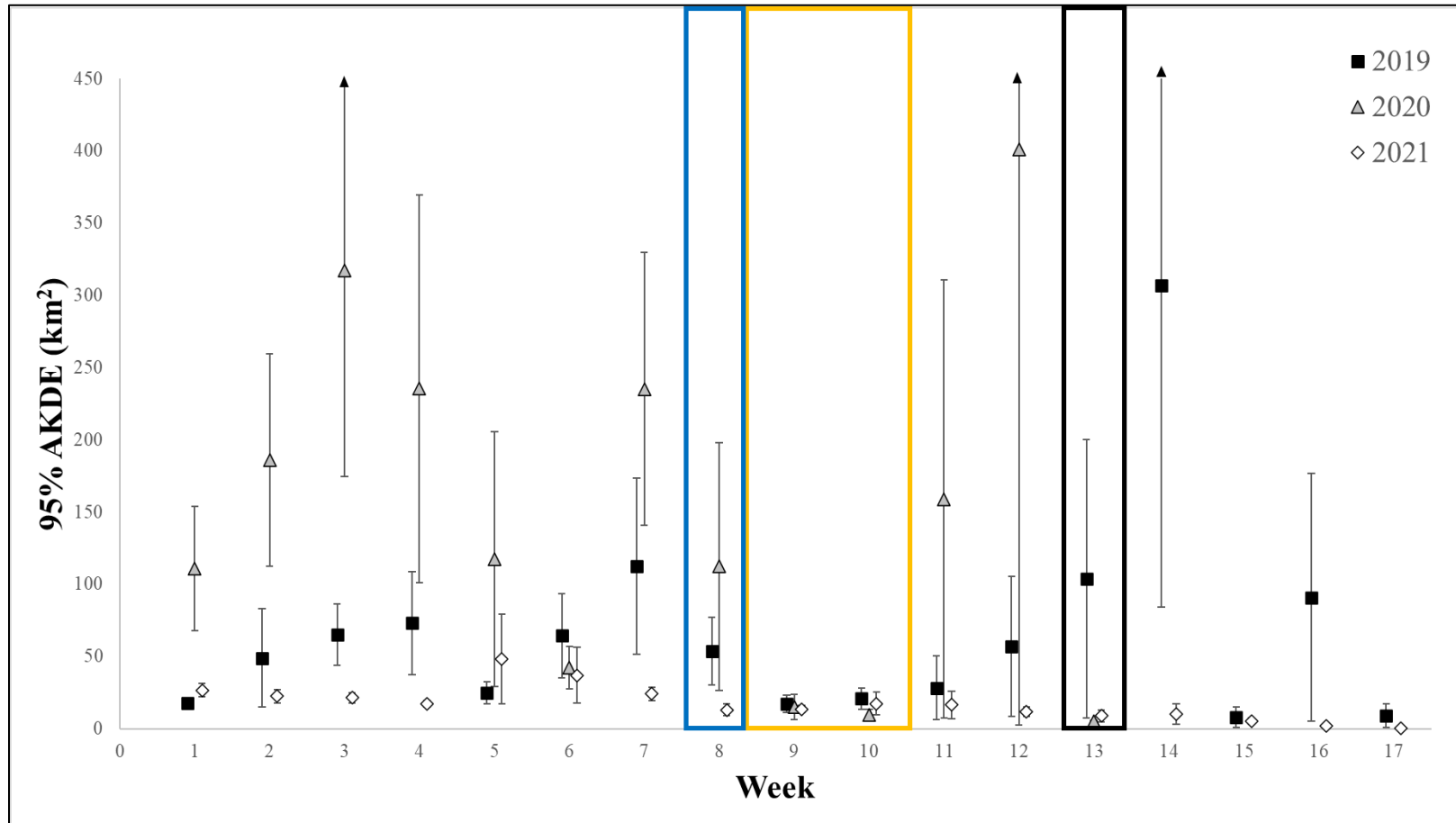


Figure 1.3. Weekly mean 95% home ranges estimates using autocorrelated kernel density estimation (AKDEs) \pm 1 SE for adult female black bears beginning 1 September (Week 1) through den entry or harvest from 2019–2021 in the Sproul State Forest, PA; colored boxes demarcate various harvest seasons (blue = muzzleloader, archery, and special firearms, orange = archery, black = firearms).

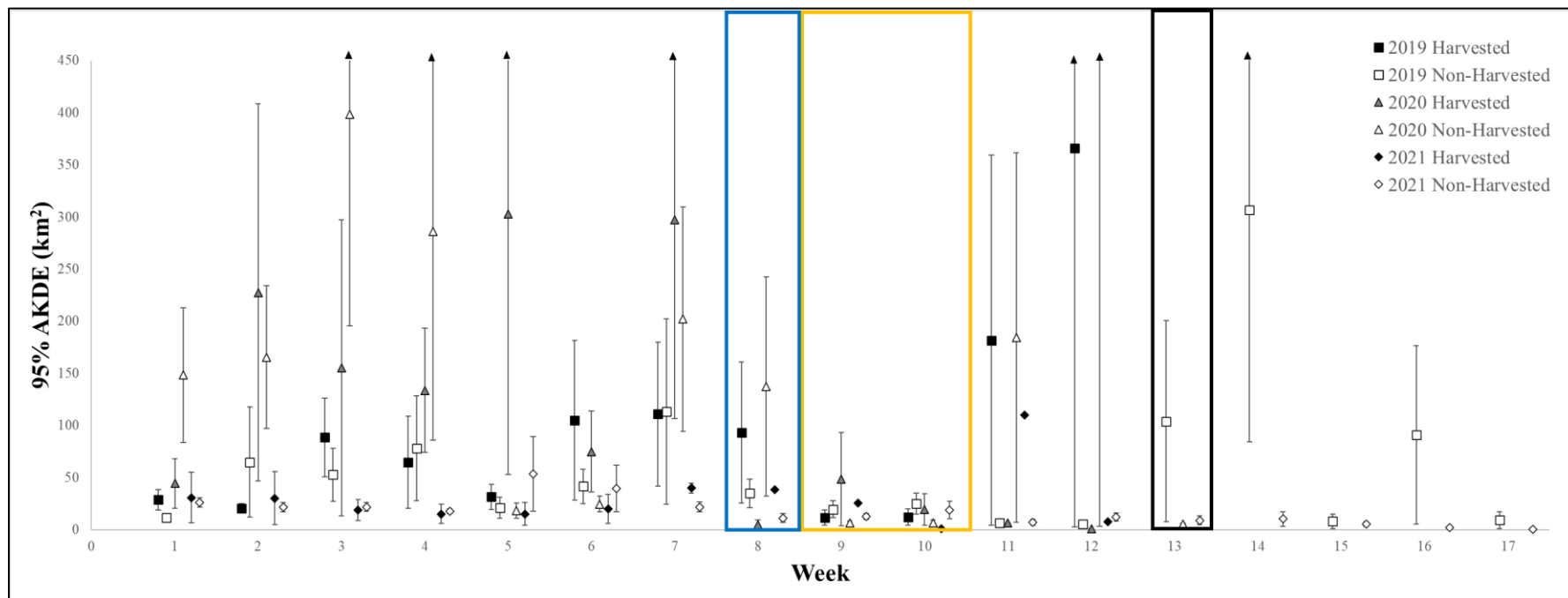


Figure 1.4. Weekly mean 95% home ranges estimates using autocorrelated kernel density estimation (AKDEs) \pm 1 SE for harvested and non-harvested adult female black bears from 1 September (Week 1) through den entry or harvest from 2019–2021 in the Sprout State Forest, PA; colored boxes demarcate various harvest seasons (blue = muzzleloader, archery, and special firearms, orange = archery, black = firearms).

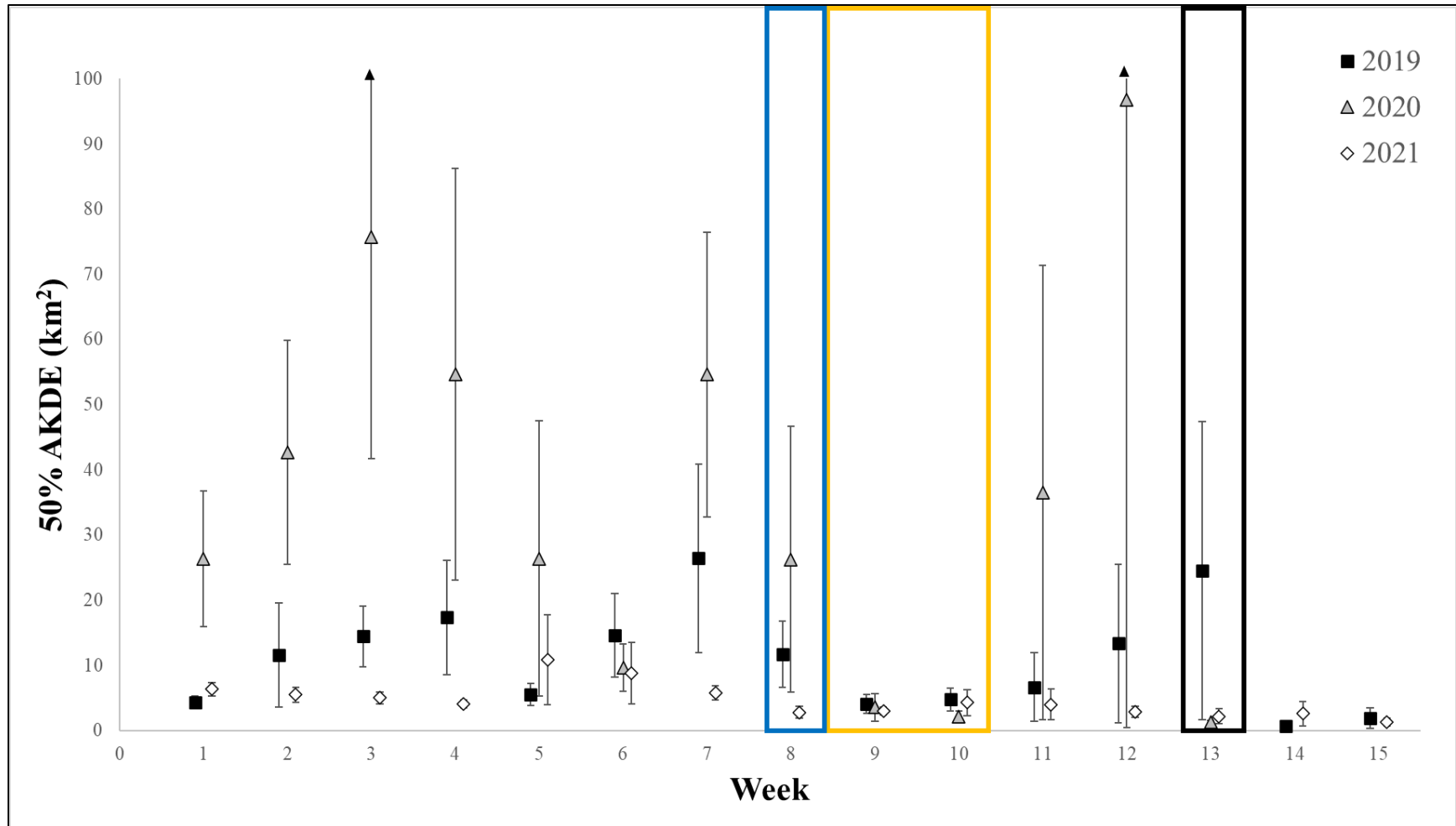


Figure 1.5. Weekly mean 50% home ranges estimates using autocorrelated kernel density estimation (AKDEs) \pm 1 SE for adult female black bears beginning 1 September (Week 1) through den entry or harvest from 2019–2021 in the Sproul State Forest, PA; colored boxes demarcate various harvest seasons (blue = muzzleloader, archery, and special firearms, orange = archery, black = firearms).

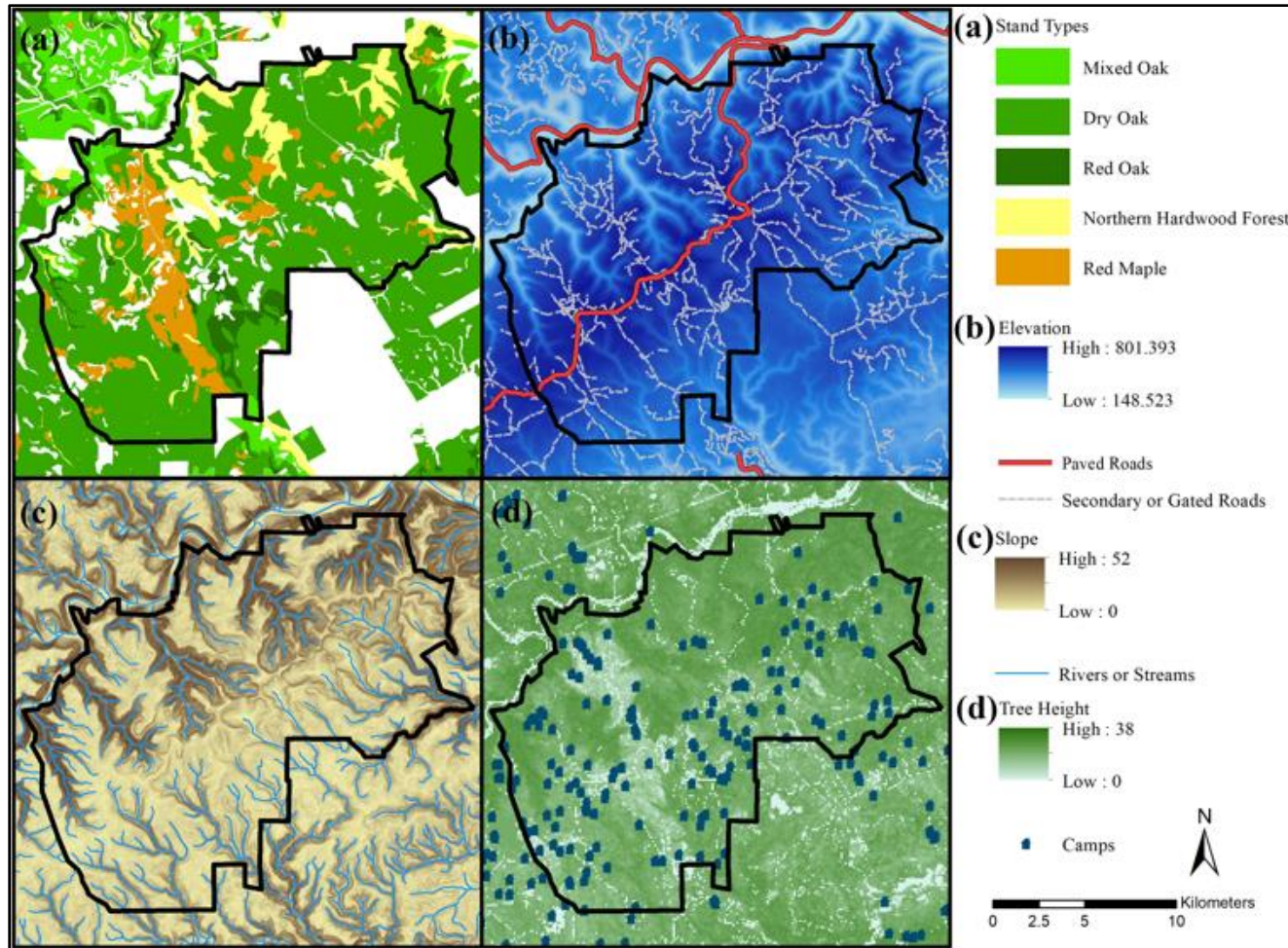


Figure 1.6. Distribution of select covariates in the most-parsimonious models of weekly resource selection by adult female black bears (*Ursus americanus*) in the Sproul State Forest in northcentral Pennsylvania.

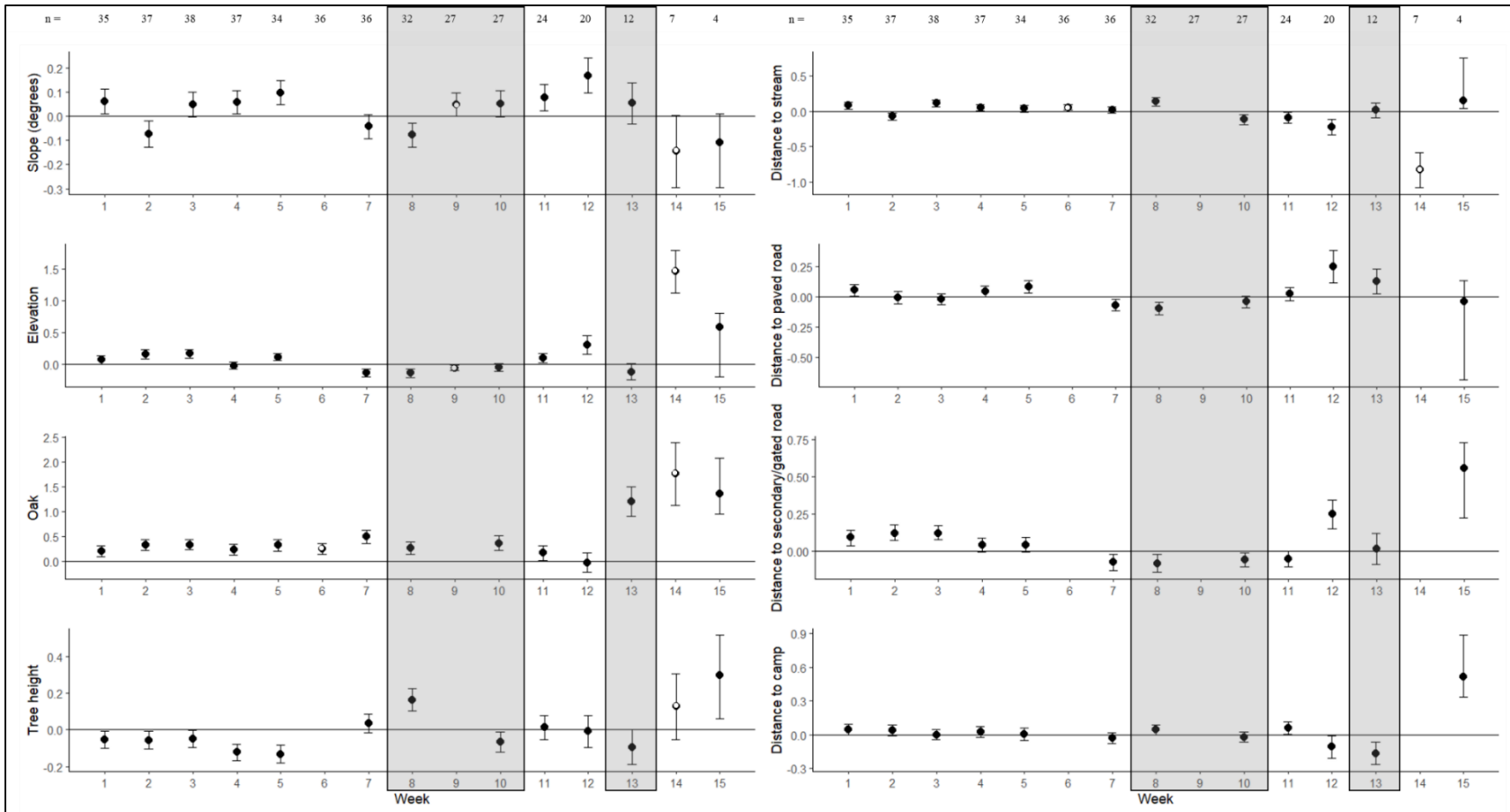


Figure 1.7. Estimated beta coefficients (β) and 95% confidence intervals from resource selection of adult female black bears (*Ursus americanus*) in the Sproul State Forest in northcentral Pennsylvania during fall (2019–2021). Week 1 began on September 1 each year. Grey boxes indicate weeks where bear harvest occurred. Black points indicate when the global model was the most-parsimonious model structure, while white points indicate a different model structure for that week. Absent values occurred when that covariate was not included in the most-parsimonious model structure for that week.

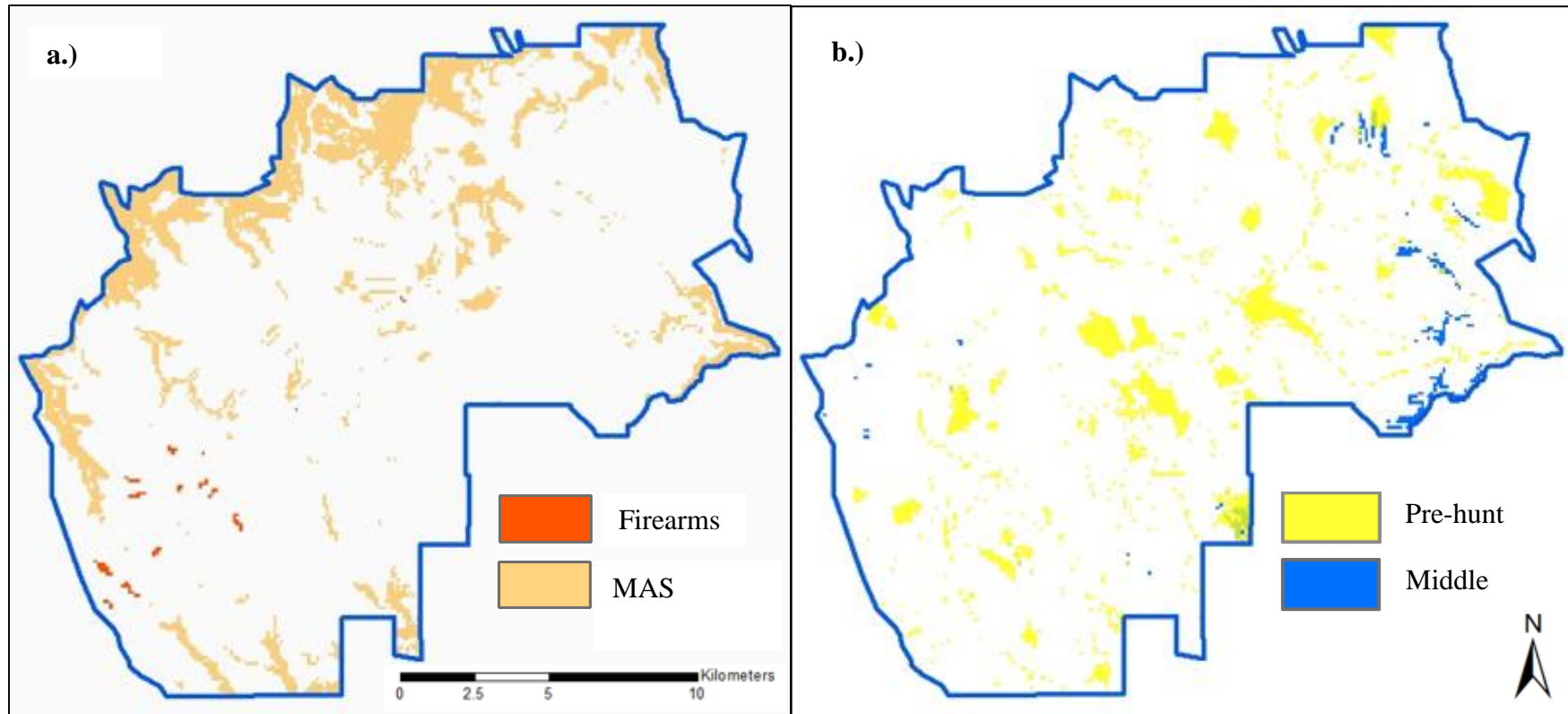


Figure 1.8. Predictive mapping of high scaled space use (>0.6) of adult female black bears (*Ursus americanus*) in the Sproul State Forest in northcentral Pennsylvania during fall (2019–2021). a.) contains predictive maps from the general firearms season (Firearms) and muzzleloader, archery, and special firearms seasons (MAS). b.) contains predictive maps from before bear hunting began (Pre-hunt) and period of no bear hunting between the muzzleloader and archery seasons and general firearms season (Middle). Green values represent regions of the study area where high scaled space use occurred in both seasons.

CHAPTER II

SURVIVAL OF ADULT FEMALE BLACK BEARS IN A MIXED-OAK HABITAT TYPE IN NORTHCENTRAL PENNSYLVANIA

INTRODUCTION

Large carnivores can have a disproportionate effect on ecosystem function, are valued as important game species (Treves and Karanth 2003), and can create human-wildlife conflict challenges for managers (Dickman 2010). Large carnivores can have indirect effects on lower trophic levels in ecosystems (e.g., reduce damage to plants by regulating herbivores; Schmitz et al. 2000), influence ecosystem processes that enhance biodiversity (Wallach et al. 2015), and may regulate ecosystem diversity by thwarting a single species from dominating a particular resource (Paine 1966). Large carnivores may regulate other species, including herbivore populations (Hairston et al. 1960), and a reduction of large carnivores can produce ecosystem and food web changes (Ripple et al. 2014). Harvesting of large carnivores could lead to population reductions (Ripple et al. 2014), but can also generate funds to support wildlife management efforts (Treves 2009). Reducing human-wildlife conflict may influence management decisions regarding these species, which may be accomplished through responsible harvest management strategies (Garshelis et al. 2020).

Organisms are inherently vulnerable to mortality from predation (or harvest), stressors, or other factors causing trauma (Scheiner and Willig 2008), and understanding causes of mortality can inform population management. Survival is a fundamental factor influencing population dynamics and can directly affect the size of populations (Williams et al 2002, Murray and Patterson 2006). Predation has a direct influence on survival and may affect other aspects of population dynamics such as reproduction and movement patterns (Williams et al 2002). Survival of large mammals can be negatively affected by anthropogenic mortality, particularly via methods of harvest (Brinkman et al 2004, Suutarinen et al. 2017, Hill et al. 2022). For carnivores, determining the sources of cause-specific mortality (e.g., disease and human activities) and cause-specific mortality rates are important to understanding the factors that limit population sizes (Boitani and Powell 2012).

Mortality and survival can be reliably estimated in free-ranging mammals through radio-telemetry studies (Millspaugh and Marzluff 2001, Murray 2006). Radio-telemetry studies can be used to determine how environmental (e.g., terrain), individual (e.g., age, sex, reproduction), and anthropogenic (e.g., harvest, road density) factors influence survival (Boitani and Powell 2012). The precision and reliability of estimated survival rates can be greatly improved in studies with radio-tracking capabilities as compared to estimates from capture-recapture data or estimates inferred from age-at-harvest survival models (Millspaugh and Marzluff 2001). The use of global positioning system (GPS) equipped radio-collars improves upon estimates derived from traditional radio-telemetry (i.e., radio-collars without GPS tracking capabilities) techniques by having greater accuracy of both the timing and location of mortality events (Hebblewhite and Haydon

2010). Through remote monitoring with satellite-linked GPS collars, estimates of survival and sources mortality of large carnivores can have improved efficiency and reliability (Moss et al. 2016, Johnson et al. 2020, Benson et al. 2023).

For long-lived carnivores such as the American black bear (*Ursus americanus*), primary causes of mortality include natural (e.g., disease, predation of younger and smaller bears, and den site flooding) and anthropogenic (e.g., harvest, poaching, control of nuisance bears, and vehicle collisions) factors (Larivière 2001, Rojas-Sereno 2022). Where hunting is permitted, harvest is the leading source of mortality of adult black bears (Kasworm and Thier 1994, Larivière 2001, Beston 2011, Gantchoff et al. 2020). When compared to black bears in western North America, bears in eastern North America typically have more stable populations, lower survival rates, and higher fecundity (Beston 2011).

In Pennsylvania, the population size of black bears has increased from ~3,500 bears in the 1970s to >20,000 bears in 2019, leading to increased bear distribution and human-bear conflict in the state (Ternent 2006). While bears are viewed as intelligent, culturally meaningful, and charismatic mammals (Kellert 1994), conflicts still occur between humans and bears, which may include threats to personal safety, property damage, vehicular collisions, and agricultural depredations (Hristienko and McDonald 2007). Human-bear conflict may be mitigated or reduced to acceptable levels by black bear population size management (Garshelis et al. 2020); therefore, harvest has been an important strategy for managing human-wildlife conflict (Lindzey 1983, Conover 2001). Although it has been suggested that a harvest rate of 15–20% may stabilize black bear populations (Bunnell and Tait 1980, Miller 1990), black bear populations in Pennsylvania

continued to increase despite consistent hunter success and annual harvest rates of 15–20% (Diefenbach et al. 2004, Ternent 2006, Carrollo 2023, unpublished data). In Pennsylvania, greater harvest rates may be required to stabilize population sizes. From 2019–2021, harvest seasons of bears in Pennsylvania increased in duration and commenced earlier in the fall than in previous years (Table 2.1). Modifications to harvest seasons included the expansion of the archery and extended rifle seasons and the establishment of the muzzleloader and the special firearms seasons (Table 2.1). Pregnant females enter winter dens earliest in Pennsylvania (Ternent 2006), which may result in earlier harvest seasons having a greater influence on reproduction due to an increased risk of mortality to pregnant females.

Here, we evaluate survival of adult female black bears and factors influencing their risk of harvest in Pennsylvania under the intensified harvest structure imposed from 2019–2021. Using location data from GPS-collared bears, we evaluated the influence of (i) different harvest seasons (e.g., archery and rifle), (ii) individual resource selection patterns, (iii) individual demographic parameters (e.g., age and reproductive status), and (iv) spatial and temporal variation in hunter activity on black bear survival rate during the period of fall harvest. We predicted that survival would be greater during harvest seasons that contained lower relative hunter activity. We predicted that survival would be greater in more rugged terrain, in older bears, and when food was abundant; we predicted that survival would be lower in bears with greater movement patterns (i.e., greater step lengths, larger home range sizes).

METHODS

Study area

Our study occurred in an approximately 308-km² study area (Figure 2.1) that was completely within the Sproul State Forest in Northcentral Pennsylvania. The entirety of the study area was open to the public for recreational activities (e.g., hunting, hiking, fishing, and camping). Some of the greatest bear harvest densities and total bear harvest in Pennsylvania have occurred in the study area (Ternent 2019). The study area was ~97% forested, which was characteristic of northcentral Pennsylvania. Mixed-oak hardwood forest was the chief cover type. Principal land uses included timber management (leading to various forest stand successional stages), natural gas extraction (leading to small, ~2 ha openings), and recreation. Hunting camps (~0.1–8 ha openings) were scattered throughout the study area. Dominant hard mast producing trees included species in both white (*Leucobalanus*) and red (*Erythrobalanus*) oak groups. Potential species competing with bears for hard mast in the fall included white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), wild turkey (*Meleagris gallopavo*), and eastern gray squirrel (*Sciurus carolinensis*).

The study area lies on the Appalachian Plateau Province and has elevations between 305–750 m. The area was composed of narrow ridges and steep slopes that had shallow soils with low fertility (NRCS 2019). Average temperatures near the study area were 11°C in fall (September–November) and -2°C in winter (December–February), and from 1981–2020 the average annual low temperature was 3.8°C, the average annual precipitation was 100.9 cm, and the average annual snowfall was 81.3 cm (US Climate Data; Renovo, PA 2020).

Capture and tracking

From late May through August of 2019–2021, we captured bears within the Sproul State Forest using barrel-style traps baited with waste pastries (Gould et al. 2021). We set up to 12 traps at a time for 8 consecutive days and checked traps daily. We sequentially trapped each of 5 regions within our study area annually.

We immobilized captured bears with either 1.0 ml/45.5 kg NalMed-A (also known as NAM; 40 mg/ml nalbuphine hydrochloride, 10 mg/ml azaperone tartrate, and 10 mg/ml medetomidine hydrochloride), 1.0 ml/45.5 kg BAM (50 mg/ml butorphanol hydrochloride, 50 mg/ml azaperone tartrate, and 20 mg/ml medetomidine hydrochloride), or a 2:0.8 mixture (only during summer capture events in 2019) of ketamine hydrochloride (4.4 mg/kg) and xylazine hydrochloride (1.8 mg/kg; Wolfe et al. 2008, Wolfe et al. 2016, Williamson et al. 2018). Immobilization drugs were delivered intramuscularly with a CO²-propelled dart. We tagged each bear in both ears with a distinctly numbered metal ear tag (style 56-L, size 36.5 × 9.5 mm; Hasco Tag Company, Dayton, Kentucky), and tattooed the inside of the upper lip for bears ≥1 year old with the lowest ear tag number. For previously captured bears, we replaced any missing ear tags.

We fitted adult female bears ≥40 kg with an iridium GPS-satellite collar (Vertex Lite with 2D battery, Vectronics, Germany) and exchanged VHF collars (ATS, Isanti, Minnesota) on bears that were previously captured by the Pennsylvania Game Commission (PGC). During each capture event, we recorded the date, location, ear tag numbers, ambient air temperature (via handheld Kestrel weather station), vital sign measurements (i.e., temperature, heart rate, and respiration rate), sex, weight, and standard physical measurements. For each adult female capture event, we additionally

recorded vulva swelling, development and condition of teats, and the presence of offspring (i.e., with cubs, with yearlings, or solitary). For adult bears of unknown age, we extracted a first upper premolar, which was used by the PGC to estimate age through cementum annuli analysis (Harshyne et al. 1998). We reversed immobilization by either an intramuscular injection of atipamezole HCL (5 mg/mg) and naltrexone HCL (1.3 mg/mg) for bears immobilized with either BAM and NalMed-A, or an intravenous injection of yohimbine hydrochloride (0.15 mg/kg) in ketamine/xylazine mixture captures. We remained near the anesthetized bear to monitor recovery and until we observed ambulatory recovery.

In February and March of 2020 and 2021, project personnel, PGC staff, or both visited winter den sites of collared adult female bears. We immobilized bears with an intramuscular injection of a 2:0.8 mixture of ketamine hydrochloride (4.4 mg/kg) and xylazine hydrochloride (1.8 mg/kg) delivered by CO²-propelled darts. We downloaded on-board location data, corrected collar fit, and replaced leather breakaway splices (to ensure collar retention across the study) on GPS collars. We did not reverse immobilization or remain at the capture location during winter den site captures to prevent abandonment of offspring. All capture and handling procedure were in accordance with guidelines endorsed by the American Society of Mammalogists (Sikes et al. 2016) and sanctioned by the Institutional Animal Care and Use Committees for South Dakota State University (Protocol 2002-005A) and Oklahoma State University (Protocol IACUC-21-19).

Survival analyses

We evaluated survival during the fall harvest seasons by using known fate models in an information-theoretic approach in program MARK (White and Burnham 1999). We considered the following factors when we assessed survival: weekly home range size, weekly mean step length, weekly mean slope, weekly mean elevation, relative hard mast abundance, year, day of year, age (continuous), harvest season, reproductive status (with offspring (1) and not with offspring (0) coded as a binary response), and indices of hunter activity to characterize harvest risk (coded as time-varying individual covariates with different effects for each harvest season; Table 2.2). We tested for correlations between continuous covariates with a Pearson's correlation coefficient using the `cor` command in R version 4.2.2 (R Core Team 2022). We considered any pair of covariates with $|r| > 0.7$ as being highly correlated (Nielsen et al. 2002). When two covariates were highly correlated, we retained the covariate that was hypothesized to have a greater influence on survival for subsequent analyses. Following the removal of correlated predictors, we developed our candidate model set by generating models for all possible additive combinations of retained predictors. We evaluated support for competing models with Akaike's Information Criterion with sample size correction (AICc; Burnham and Anderson 2002). Using the most-parsimonious model, we assessed both daily and fall (across all harvest seasons each year) survival probabilities. We censored bears in analyses as they either entered a den or experienced collar malfunction. We visualized daily survivorship with Kaplan-Meier survival curves (Kaplan and Meier 1958, Rich et al. 2010) with the `survival` package in R (Therneau 2020) for both fall (i.e., each year) and total (i.e., across years) survival. We assessed beta coefficients (with 85%

confidence intervals, CIs; Arnold 2010) for predictors in the most-parsimonious model. We calculated yearly and overall (a combination of all years) harvest rates by dividing the number of GPS-collared bears harvested by the total number of GPS-collared bears that were alive during the commencement of bear harvest seasons.

Space-use covariates

We considered covariates on survival related to space use and third-order resource selection patterns of adult female bears in our study system, including home range size, slope, elevation, and step length. We assessed space-use covariates weekly from 1 September until mortality or den entry. During harvest seasons, we used 50% weekly home range size estimates generated with auto-correlated kernel density estimation (Chapter I). Additionally, slope and elevation were identified as the only covariates included in the most-parsimonious model of weekly resource selection across all weeks where harvest occurred, but patterns of selection for these covariates varied among weeks (Chapter I). We obtained elevation (m) and slope (degrees) from 2020 LANDFIRE (<https://landfire.cr.usgs.gov/>) by the Extract Multi Values to Points tool in ArcMap 10.8.1 (ESRI, Redlands, CA). We determined the mean elevation and mean slope from all GPS locations within each week for each bear. We estimated weekly mean step lengths (distance between locations) from all GPS locations within 50% home range estimates for each bear, and we performed this analysis on MoveApps (www.moveapps.org, Scharf 2022). Bears that were harvested usually had too few points during the week of harvest to adequately characterize space-use patterns. Consequently, we used covariate estimates for home range size, elevation, slope, and step length from the previous week.

Mast surveys and analyses

We estimated percent crown containing acorns (PCA) of mast producing trees in late summer in 2019–2021 (Greenberg and Warburton 2007). We selected 10 random transect starting locations (Figure 2.1) and then systematically established 1.6-km transects that were overlaid on existing roads in the study area and maintained each year. We surveyed each transect once annually by stopping at 0.16-km intervals and assessing the PCA of dominant hard mast-producing trees (*Quercus* spp.) within sight of the vehicle. At each of the 11 stopping points within each transect, we randomly selected 4 trees and recorded their species, diameter breast height (DBH), and PCA score. We did not identify or mark individual trees within transects so an identical sample of trees were not used between years. We also assessed PCA of five permanent hard mast plots (Figure 2.1) during the same time frame that were previously established on the study area. These plots contained approximately 50 trees, and within these plots, we sampled identical trees from 2019–2021.

We used the product of DBH and PCA to produce a relative hard mast score for each tree that was sampled. We grouped hard mast-producing trees into two groups: red oaks (*Erythrobalanus*) and white oaks (*Leucobalanus*). To assess the effect of year and family on hard mast abundance, we employed a Kruskal-Wallis test (Kruskal and Wallis 1952) to assess the effect of year and a Wilcoxon signed-rank test (Wilcoxon 1945) to assess the effect of the interaction between year and family. All hard mast production analyses were completed in R.

Hunter space-use surveys and analyses

To quantify the potential risk of bears encountering a hunter, we established surveys to index temporal and spatial variation in hunter activity. To assess temporal patterns, we conducted road transects to index hunter activity patterns during each harvest season within each year from 2019–2021. In 2019, we systematically distributed 10 transects, each 4.8 km with a randomized starting location, across the study area (Figure 2.2). We conducted surveys in the morning hours (~0800–1200) while driving ≤ 40 kilometers per hour. We completed each survey in ~10 minutes. Each year, we surveyed each transect multiple times during each bear hunting season (Table 2.3). During surveys, we recorded the number of hunters within 30 m of the transect, parked vehicles, moving vehicles, and minimum counts of individuals within moving vehicles.

To evaluate spatial variability in hunter space use across the study area, we used motion-triggered cameras and an occupancy modeling framework (MacKenzie et al. 2002) to estimate the probability of hunter use. We divided the study area into 1-km² cells and randomly selected (without replacement) 80 cells (hereafter, sites) to sample (Figure 2.2). We deployed a motion-triggered camera (Bushnell Trophy Cam or cellular Bushnell Impulse) within each site and sampled during bear hunting seasons (Table 2.1) in 2020 and 2021. We developed daily encounter histories for humans at each camera, where a human detection (1) and non-detection (0) was coded as a binary response. Due to an inability to confidently differentiate bear hunters, deer hunters, or hikers in photographs, all humans (excluding our research team) were classified together.

We estimated patterns of detection and space use for humans across the study area with a single-season occupancy approach (MacKenzie et al. 2002). We assumed that

hunter occupancy was not closed to changes (i.e., whether hunters were present within a grid cell could change over the sampling period) and that space-use patterns of humans was similar across years (i.e., areas with high human use in one year were also likely to experience high human use in other years). Consequently, we combined data for sites sampled in 2020 and 2021 into a single analysis and interpreted estimates for occupancy as estimates of the probability of use during the fall sampling period (MacKenzie et al. 2018). We modeled the probability of detection (p) for humans as a function of covariates expected to influence human activity levels (i.e., rainfall and temperature) or differences due to sampling equipment (i.e., camera type). We obtained daily total rainfall (cm) and minimum daily temperature (Celsius) from NOAA (National Oceanic and Atmospheric Administration, NOAA 2022).

We hypothesized that the relative probability of space use (ψ) of hunters may be influenced by elevation, slope, distance to stream or river, or distance to secondary road. There is evidence that hunters targeting large mammals may have a high probability of use in areas that are closer to roads and trails and variable probability of use for slope and distance to stream based on harvest season and hunter success (Rowland et al. 2021). Hunters may target these areas based on accessibility and topographic relief (Rowland et al. 2021). Additionally, elevation was included in our analysis because hunters of large mammals may select for areas of lower elevation (Rosenberger et al. 2022) and the most remote portions of our study area generally occurred areas with some of the lowest elevation values. We used the same LANDFIRE layers for elevation (m) and slope (m/m) as previously described. We generated a covariate for distance to stream or river (m) from merging stream and river shapefiles from LANDFIRE and using the “Near” tool in

ArcMap. Similarly, we estimated distance to secondary road (m) from a shapefile provided by the Pennsylvania Department of Conservation and Natural Resources. We tested for pairwise correlations between covariates that were predicted to influence detection and between covariates that were predicted to influence human space use; we considered covariates to be highly correlated based on Pearson's correlation coefficient (i.e., $|r| > 0.7$).

Preliminary analyses (not reported) indicated that human space use was widespread across the study area (i.e., probability of use ~ 1). Consequently, to characterize spatial variation in the relative intensity of use, we reconstructed our daily encounter history to characterize $\geq n$ independent human detections as a detection (1) and $< n$ human detections as a non-detection (0). We increased n until a pattern of variation of space use was detected. We characterized independent detections as 30 minutes between detections. We evaluated space use of hunters using an information-theoretic approach in program MARK (White and Burnham 1999). We developed our candidate model set by generating all possible combinations of models (contained both covariates for p and ψ). We evaluated support for competing models with Akaike's Information Criterion with sample size correction (AICc; Burnham and Anderson 2002). We assessed beta coefficients (with 85% confidence intervals, CIs; Arnold 2010) for predictors in the most-parsimonious model. We used the most-parsimonious model to create a predictive raster for human space use (Figure 2.2).

Finally, to generate our risk covariate, we multiplied the index of hunter activity (i.e., hunters/day from road surveys) for each season and year (Table 2.3) by the predictive raster that characterized hunter space use during harvest seasons (Figure 2.2).

We then divided the values within all predictive rasters by the greatest value from among all of the rasters to scale each raster from 0–1, where greater values equate to greater scaled use. We calculated a mean value from each bear’s weekly used points (from the previous week) within their 50% home ranges during each associated harvest season.

RESULTS

Capture and tracking

We deployed traps in identical locations each year from 29 May–20 August 2019, 28 May–18 August 2020, and 2 June–27 July 2021. We observed a decrease in trapping success from 26% in 2019 to 20% in 2020 and 14% in 2021, which resulted in a decrease in bears captured with 70, 57, and 39 bears being captured each year, respectively. Mean collared bear age was 7.1 years (SD = 4.56, range = 1–20), and there were 15 collared bears with offspring during the harvest seasons. Mean 50% home range estimates were 57.97 km² (SD = 183.6, range = 0.16–1597.31). Mean step lengths were 57.8 m (SD = 28.6, range = 26.5–266.0). We observed a decrease in the total number of collared bears from 30 in 2019 to 29 in 2020 to 20 in 2021, with a total of 45 collared individuals from 2019–2021. There was an increase in the number of collared bears that experienced mortality events or collar malfunctions prior to the start of bear harvest seasons from one each in 2019 and 2020, to four in 2021. Due to mortality events or collar malfunctions, we only assessed survival for 28 bears in 2019, 24 bears in 2020, and 16 bears in 2021. The number of GPS-collared bears and harvested individuals decreased over the course of the study (Table 2.4). Fewer collared bears experienced harvest mortality during archery seasons than any other harvest seasons, despite archery being the longest harvest season each year (Table 2.4).

Mast surveys and analyses

We estimated PCA of mast producing trees during 27 August–6 September 2019, 24 August–1 September 2020, and 16 August–21 August 2021. Overall relative hard mast varied by year and declined over the course of the study (Figure 2.3). Relative hard mast estimates (PCA * DBH) were 9.45 (SE = 1.07) in 2019, 7.15 (SE = 0.96) in 2020, and 1.83 (SE = 0.35) in 2021 for all surveyed trees. Estimates for red oaks declined over the course of the study and were much lower in 2021 than in 2019 or 2020. Estimates for white oaks increased over the course of the study and were much greater in 2021 than in 2019 or 2020. Red oaks had more relative hard mast than white oaks in 2019 and 2020, while white oak estimates were greater in 2021 (Figure 2.3).

Hunter space-use surveys and analyses

Indices of hunter activity indicated temporal and spatial variation. Roadside surveys indicated hunters/day was lowest in 2019 and greatest in 2020 (Table 2.3). During the muzzleloader and archery harvest seasons, the index of hunters/day was lowest in 2021 and greatest in 2020. In contrast, the greatest index of hunters/day in the general firearms season occurred in 2021. The greatest index of hunters/day occurred during the earlier muzzleloader and archery harvest seasons in 2020 and corresponded to the year with the lowest index of hunters/day during the later general firearms season (Table 2.3). We detected humans across the majority (85%) of sites monitored with cameras. When we characterized a detection as $n \geq 2$ independent human detections, our most-parsimonious model for human space use was the null model (i.e., no spatial variation in use). When we characterized a detection as $n \geq 3$ independent human detections, our most-parsimonious model (AIC weight = 0.049, $-2\text{Log(L)} = 300.369$)

indicated rain ($\beta = -2.186$, SE = 1.591, 85% CI = -4.477, 0.105) and rifle season ($\beta = 2.328$, SE = 0.360, 85% CI = 1.810, 2.846) were associated with detection, whereas elevation ($\beta = 7.90$, SE = 5.13, 85% CI = -0.52, 15.28) was positively associated with areas of high human space use (Table 2.5, Figure 2.2). Although there was some model uncertainty (i.e., the next closest model was separated from the most-parsimonious model by $\Delta 0.22$ AICc), we were interested in developing a predictive surface for human space use and therefore used the most-parsimonious model.

Survival analyses

Harvest mortality decreased annually. Aside from one bear that died from a vehicle collision in 2019, all mortality events were due to harvest. The harvest rate of collared bears was 0.345 in 2019, 0.321 in 2020, and 0.150 in 2021, and averaged 0.272 across all three years. During the fall, Kaplan-Meier survivorship was 0.533 in 2019, 0.505 in 2020, 0.767 in 2021, and averaged 0.574 across all three years. Daily survivorship was lowest in 2020 and greatest in 2021 (Figure 2.4). Daily survivorship was lowest during the muzzleloader, archery, and special firearms seasons in 2020 and was greatest in 2021 during the same period (Figure 2.4).

Mean elevation was correlated with risk ($|r| = 0.978$), so we excluded elevation from our predictor set and established a global model including additive effects of home range size, mean step length, mean slope, relative hard mast abundance, year, bear age, harvest season, reproductive status, and risk. There were 11 competitive models within 2 Δ AICc (Table 2.6) that included bear age, relative hard mast abundance, mean slope, risk, season, offspring, and weekly home range sizes. The most-parsimonious model contained bear age, relative hard mast abundance, mean slope, and risk (Table 2.7). From

our most-parsimonious model (Table 2.6), the probability of surviving all harvest seasons in any given year was 0.611 (SE = 0.086, 95% CI = 0.436, 0.761). Daily probability of survival during harvest seasons was lowest during the general firearms harvest season and greatest during the archery harvest season (Figure 2.5). Based on the most-parsimonious model, survival was lower in older age bears, lower when mast was more abundant, lower in steeper slopes, greater in areas of greater human space use (risk) during archery harvest season, and lower in areas of greater human space use (risk) during the general firearms harvest season (Table 2.7, Figure 2.6).

DISCUSSION

Harvest of carnivores can lead to declines in population densities and at high levels may cause local extirpations (Peterson et al. 1984, Rolley 1985). Compared to many terrestrial mammals, species in *Ursus* have lower rates of reproduction (Bunnell et al. 1981), which may not allow for rapid responses to population declines. In Pennsylvania, the population estimates of bears decreased each year from 2019–2021 (Carrollo 2022). Harvest rates for all bears in Pennsylvania during the statewide muzzleloader, archery, special firearms, and general firearms seasons collectively declined from 20.8% in 2019 to 20.1% in 2020 to 18.2% in 2021 (Carrollo 2022). Harvest rates for all female bears in Pennsylvania were ~13% from 2010–2018, ~19% in 2019 to ~20% in 2020 to ~20% in 2021 (E. Carrollo, personal communication). Our harvest rates for collared adult females over the same period were greater than statewide harvest rates in 2019 and 2020, and lower in 2021. Higher harvest rates may indicate that in our study system, adult female bears were affected by harvest on a more localized scale. One potential difference that may have affected harvest rates was that our study

area was not open to the extended bear hunting season (Table 2.1), which occurred concurrently with Pennsylvania's white-tailed deer (*Odocoileus virginianus*) firearms seasons. The timing and duration of harvest seasons could have caused bear hunters to be afield more frequently during the shorter total harvest season lengths, leading to higher harvest rates observed by our study. Bears in our study area had higher daily probabilities of survival during archery season, which may have been a result of lower bear hunter engagement during this period. The first seven days and last four days of harvest had lower estimates of daily survival. These lower estimates may be a result of methods of take with more effective ranges and more hunters afield in these seasons. Additionally, six of 29 (~20.7%) collared bears in 2019 survived the duration of the study, which was comparable to the probability of surviving all harvest seasons for three years (~22.8%) in our most-parsimonious model. From 2019–2021, bear hunter success was ~1.87% (Carrollo 2022), which was below the 10-year mean (~2.2%) prior to the inception of this study (Ternent 2019). There was an increase of bear hunting license sales in 2019–2021 from the number of license sales in 2017–2018 (Carrollo 2022). Species management has the potential to cause a decrease in hunter interest (Enck et al. 1993). If decreased hunter success is a result of increasing bear hunting opportunities, negative impressions of expanded harvest seasons may occur.

Harvest may influence population dynamics by disrupting age structures in the population (Milner et al. 2007). Vulnerability to harvest typically decreases with age in female bears (Ternent 2006) and may be, at least in part, due to younger bears entering winter dens later (Tietje and Ruff 1980), making them more vulnerable to harvest for a longer period. However, our results showed support for older female bears experiencing a

reduced probability of survival. This may be a result of two factors influencing survival: (i) prior timing of harvest seasons (i.e., occurring later in the fall) have protected older females as they may have entered winter dens prior to the commencement of bear harvest seasons (Alt 1980), and (ii) older mammals tend to decrease in overall health when they age (Ricklefs 2010) and therefore may have a reduced ability to avoid hunters.

Areas with steep slopes may function as refugia from hunters (Diefenbach et al. 2005). However, hunter success of harvesting large mammals during certain seasons may be related to steeper slopes, potentially due to topographic relief (Rowland 2021). Therefore, hunters may select hunting locations based on method of take and environmental visibility (Rowland 2021). Bears have selected for steeper terrains, as hunters may not opt to hunt in these areas due to the challenging nature of both movement and harvested game recovery (Jones et al. 2015). Our results showed evidence for predicted survival of bears being lower in areas of steeper slopes, which may indicate that successful bear hunters are selecting for steeper slopes that were used more by bears during certain weeks of harvest (Chapter I). Successful bear hunters may be recognizing high use areas of bears and subsequently harvesting in higher rates in these areas. Additionally, although slope was not in the most-parsimonious model for hunter space use, there could be an unobserved relationship between slope and hunter use in our study system. This potential discrepancy in hunter space use may be attributed to our sampling method for trail camera site selection, as selected sites may have been functioning more as corridors for bear hunters rather than intensely hunted areas.

Poor fall food abundance conditions, namely acorn mast production, can lead to larger movements and decreased survival (Pelton 1989). Evidence exists for earlier den

entry by bears in years with poorer food conditions (Johnson and Pelton 1980). However, bears in our study system entered dens later in the year (2021) with the poorest hard mast conditions. Additionally, mortality may be greater in years with poor food conditions, as human-wildlife conflict can increase in those circumstances (Rogers 1976). Since bears cannot be harvested in dens in Pennsylvania, they are inherently more vulnerable to mortality through harvest by entering winter dens later. However, our results indicated that there was evidence that survival was greater during years with poorer acorn abundance and later den entrance. A potential explanation of this trend may be that animals will attempt to maximize energy acquired or curtail time spent on energy acquisition (Pyke et al. 1977). During poor mast conditions, bears may be minimizing exploratory trips (in search of greater food resources), which would minimize energetic efforts to acquire resources and potentially exposure to hunters. Therefore, bears may be less likely to expand home range sizes and move core home range areas during these conditions. Our data show support for this association, as 2021 experienced the poorest hard mast conditions while also having the smallest home range estimates (Chapter I).

Animals may change their behavior as a reaction to the risk of predation (Laundré et al. 2010). Black bears may avoid areas where there is a higher perceived risk (Stillfried et al. 2015). There was evidence that survival was higher in areas where risk was greater during archery season, but survival was lower in areas where risk was greater during the general firearms season. The trend observed in the archery season may be a product of very low risk values (relative to other seasons) due to lower number of hunters observed in transects. Bears were selecting for lower elevations during the general firearms season (Chapter I), while during the same period the higher risk areas were leading to lower

probabilities of survival. This pattern supports the premise that bears were avoiding areas that they were most likely to experience mortality in during the general firearms season.

Management implications

Survival of female bears may be influenced by age, fall food conditions, slope, and risk associated with an index of hunting pressure during bear harvest seasons. Bear harvest seasons receive strong public scrutiny (Loker and Decker 1995). Public opposition or criticism of bear harvest seasons may be curtailed if managers used improved season-specific survival data to justify decisions on timing and duration of bear harvest seasons. For bears, refugia are necessary to limit accessibility to humans, especially during harvest seasons (Powell et al. 1996). In our study area, adjusting the quantity of remote areas during harvest seasons could be accomplished through limiting access to secondary or gated roads, which are generally openly accessible during bear harvest seasons. Older adult females generally produce larger litters (Alt 1982) and therefore a decrease in predicted survival in older individuals may intensify alterations to population dynamics, which may help managers achieve current population management objectives but may have prolonged effects on population size. Additionally, hard mast data are collected prior to bear harvest seasons each fall and could be used as an indicator of upcoming harvest susceptibility for adult female bears, allowing managers to potentially adjust harvest seasons (e.g., timing or lengths of seasons) annually to account for variation in fall food abundance and achieve management objectives.

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TABLES

Table 2.1. Summary of 2018–2021 black bear (*Ursus americanus*) harvest seasons in Pennsylvania.

Season	2018		2019		2020		2021	
	Season Dates	Days	Season Dates	Days	Season Dates	Days	Season Dates	Days
Archery	Oct. 29 – Nov. 3	6	Oct. 28 – Nov. 9	12	Oct. 17 – Nov. 7	19	Oct. 16 – Nov. 6	19
Muzzleloader	No Season	0	Oct. 19 – Oct. 26	7	Oct. 17 – Oct. 24	7	Oct. 16 – Oct. 23	7
General	Nov. 17 – Nov. 21	4	Nov. 23 – Nov. 27	4	Nov. 21 – Nov. 24	4	Nov. 20 – Nov. 23	4
Special Rifle	No Season	0	Oct. 24 – Oct. 26	3	Oct. 22 – Oct. 24	3	Oct. 21 – Oct. 23	3
Extended Rifle	Nov. 26 or 28 – Dec. 1	4 or 6	Nov. 30 – Dec. 7	7	Nov. 30 – Dec. 5	6	Nov. 27 – Dec. 4	8
Total Hunting Days		14 or 16		30		29		31
Earliest Start Date		Oct. 29		Oct. 19		Oct. 17		Oct. 16

Table 2.2. Covariates considered for known-fate survival modeling for adult female black bears (*Ursus americanus*) in the Sproul State Forest in northcentral Pennsylvania during fall (2019–2021). Positive (+) and negative (-) predictions indicated that these covariates were expected to have a positive or negative association with survival. Season covariates are ranked based on their predicted effect on survival with more “-“ indicating lower predicted survival.

Category	Covariate	Prediction
Space use	Home range size	-
	Step length	+
	Slope	-
Life history	Age	+
	With offspring	-
Food conditions	Acorn mast	+
Temporal	Year	+
	Risk	-
	Harvest seasons	
	Muzzleloader/Archery	--
	Muzzleloader/Archery/Special Firearms	---
	Archery	-
	General Firearms	----

Table 2.3. Summary of hunter transect surveys in the Sproul State Forest from 2019–2021; surveys were conducted in the morning hours (~0800–1200) while driving ≤ 40 kilometers per hour, and each survey was completed in approximately 10 min. In 2019, we surveyed transects four times during muzzleloader season (19 – 26 October), 11 times during archery season (28 October – 9 November), and four times during the general firearms season (23 – 27 November). In 2020, we surveyed transects three times during muzzleloader/archery season (17 – 24 October), three times during archery season (25 October – 7 November), and four times during the general firearms season (21 – 24 November). In 2021, we surveyed transects six times during muzzleloader/archery season (16 October–23 October), twelve times during archery season (24 October–6 November), and four times during the general firearms season (20 November–23 November).

Season	Hunters/day			Parked/Day			Driving/day			Individuals/Day		
	2019	2020	2021	2019	2020	2021	2019	2020	2021	2019	2020	2021
Muzzleloader ^A	2.5	6.67	1.82	9.25	20.00	8.36	6.75	7.33	6.00	9.75	9.67	8.18
Archery	0.27	2.33	0.42	5.64	5.67	3.75	4.36	4.33	3.25	5.73	6.00	4.00
General Firearms	6.75	5.25	9.25	21.75	22.00	22.00	11	9.75	2.25	22	13.25	11.25
Mean	3.17	4.75	3.83	12.21	15.89	11.37	7.37	7.14	3.83	12.49	9.64	7.81

^AMuzzleloader/Archery season in 2020 and 2021

Table 2.4. Number of GPS-collared adult female black bears (*Ursus americanus*) harvested and present in each harvest season during 2019–2021 harvest seasons in the Sproul State Forest, PA.

Year	Harvest Season	Harvested	Bears
2019	Muzzleloader/Special Firearms	4	29
	Archery	3	25
	General Firearms	3	22
	Total	10	
2020	Muzzleloader/Archery/Special Firearms	7	28 ^A
	Archery	1	21
	General Firearms	1	20
	Total	9	
2021	Muzzleloader/Archery/Special Firearms	1	16 ^B
	Archery	0	15
	General Firearms	2	13
	Total	3	

^AGPS collars on 1 of 29 bears stopped transmitting data prior to the start of bear harvest

^BGPS collars on 4 of 20 bears stopped transmitting data prior to the start of bear harvest

Table 2.5. Model selection results of occupancy estimation models for detection (p) and space use (ψ) of humans during 2020–2021 bear harvest seasons in the Sproul State Forest, PA.

Detection Model	Occupancy Model	AICc	Δ AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
$p \sim$ Rain + Rifle	$\psi \sim$ Elevation	311.23	0.00	0.049	1.00	5	300.37	300.37
$p \sim$ Rain + CamType + Rifle	$\psi \sim$ Elevation	311.45	0.22	0.044	0.896	6	298.23	298.23
$p \sim$ Rifle	$\psi \sim$ Elevation	311.78	0.55	0.037	0.760	4	303.21	303.21
$p \sim$ CamType + Rifle	$\psi \sim$ Elevation	311.94	0.71	0.034	0.701	5	301.08	301.08
$p \sim$ Rain + Rifle	$\psi \sim$ Null	311.95	0.73	0.034	0.696	4	303.39	303.39
$p \sim$ Rain + Rifle + CamType	$\psi \sim$ Null	311.99	0.76	0.033	0.684	5	301.13	301.13
$p \sim$ Temp + Rain + Rifle	$\psi \sim$ Elevation	312.55	1.32	0.025	0.517	6	299.33	299.33
$p \sim$ CamType + Rifle	$\psi \sim$ Null	312.59	1.37	0.025	0.505	4	304.03	304.03
$p \sim$ Rifle	$\psi \sim$ Null	312.63	1.40	0.024	0.496	3	306.30	306.30
$p \sim$ Temp + Rain + CamType + Rifle	$\psi \sim$ Elevation	312.72	1.49	0.023	0.474	7	297.07	297.07

Note: Rain = rainfall (cm), Rifle = Rifle bear harvest season, Elevation = Elevation (m), CamType = Camera Type, Temp = Temperature ($^{\circ}$ C)

Table 2.6. Model selection results of known-fate models for survival (ϕ) of GPS-collared adult female black bears during 2019–2021 bear harvest seasons in the Sproul State Forest, PA.

Model	AICc	Δ AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
$\phi \sim$ Age + Mast + Slope + Risk	202.07	0	0.022	0.999	8	185.94	185.94
$\phi \sim$ Season + Age + Mast + Slope	202.57	0.50	0.017	0.779	7	188.47	188.47
$\phi \sim$ Age + Mast + Offspring + Slope + Risk	203.11	1.04	0.013	0.595	9	184.94	184.94
$\phi \sim$ Age + Slope + Step	203.15	1.08	0.013	0.583	7	189.05	189.05
$\phi \sim$ Season + Age + Slope	203.32	1.25	0.012	0.535	6	191.25	191.25
$\phi \sim$ Age + Mast + Risk	203.47	1.40	0.011	0.497	7	189.36	189.36
$\phi \sim$ Age + Mast + Slope + Step	203.54	1.47	0.011	0.480	8	187.41	187.41
$\phi \sim$ Age + Slope + Risk	203.62	1.55	0.010	0.460	7	189.52	189.52
$\phi \sim$ Season + Age + Mast + Offspring + Slope	203.83	1.76	0.009	0.415	8	187.69	187.69
$\phi \sim$ Age + Mast + Slope + HR + Risk	203.89	1.82	0.009	0.403	9	185.72	185.72
$\phi \sim$ Mast + Offspring + Slope + Risk	203.95	1.89	0.009	0.390	8	187.82	187.82

Note: Age = age in years (continuous), Mast = relative hard mast abundance (with higher relative hard mast (1) and lower relative hard mast (0) coded as a binary response), Slope = weekly mean slope (degrees), Risk = indices of hunter activity (coded as time-varying individual covariates with different effects for each harvest season), Season = bear harvest seasons, Offspring = reproductive status (with offspring (1) and not with offspring (0) coded as a binary response), HR = weekly home range size.

Table 2.7. Beta estimates, standard error, and 85% confidence intervals of the most-parsimonious known-fate model of GPS-collared adult female black bears during 2019–2021 bear harvest seasons in the Sproul State Forest, PA.

Parameter	Beta	Standard Error	85% Lower	85% Upper
Intercept	6.068	1.072	4.524	7.612
Age	-0.107	0.049	-0.178	-0.036
Mast	-1.235	0.722	-2.274	-0.195
Slope	-0.050	0.026	-0.088	-0.012
Risk1	-0.092	2.059	-3.056	2.871
Risk2	-0.124	2.417	-3.603	3.356
Risk3	37.650	24.335	2.619	72.682
Risk4	-2.414	1.298	-4.282	-0.546

FIGURES

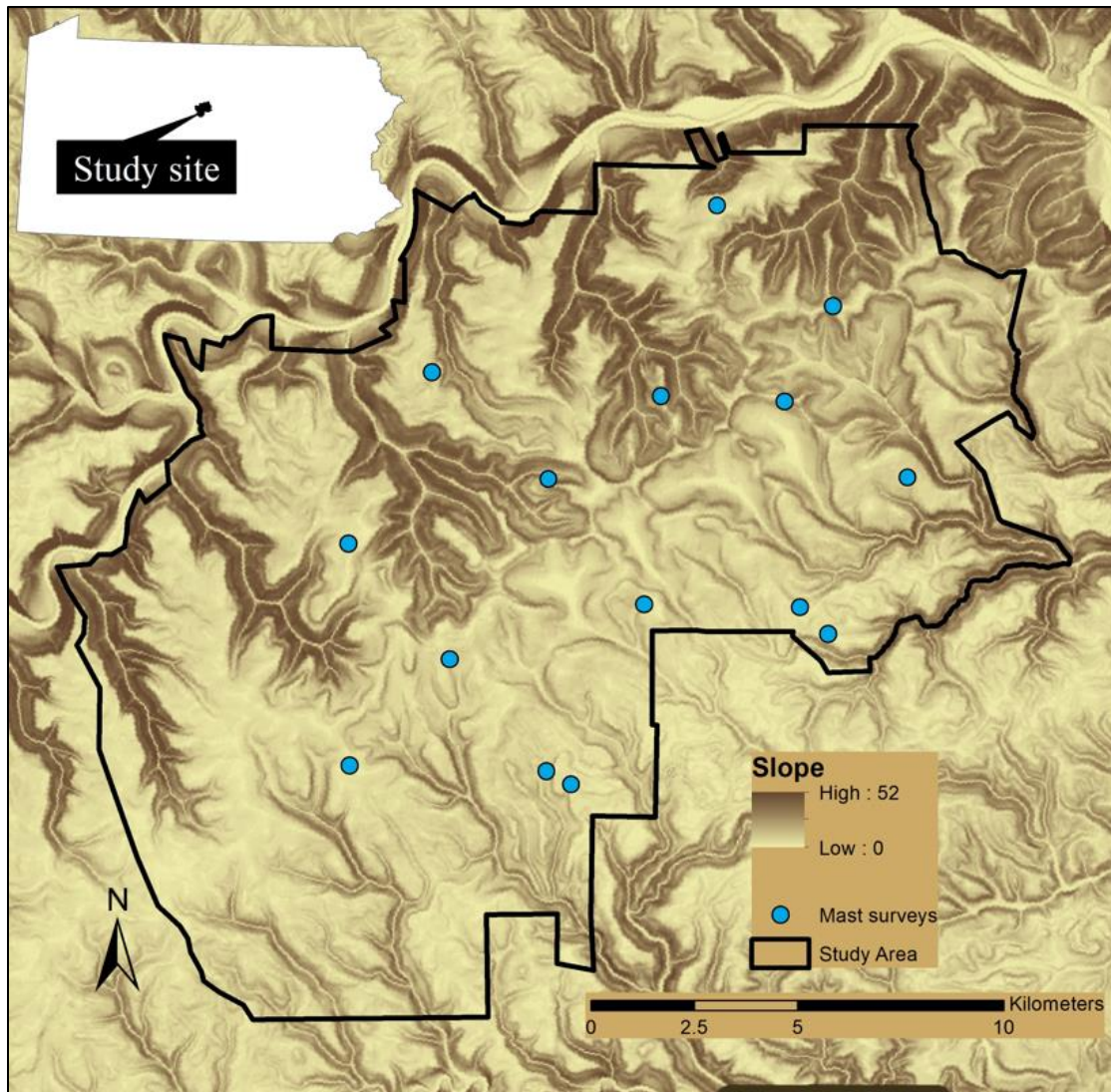


Figure 2.1. Location of the American black bear (*Ursus americanus*) study area, slope (degrees), and mast survey locations during fall (2019–2021) in the Sproul State Forest in northcentral Pennsylvania.

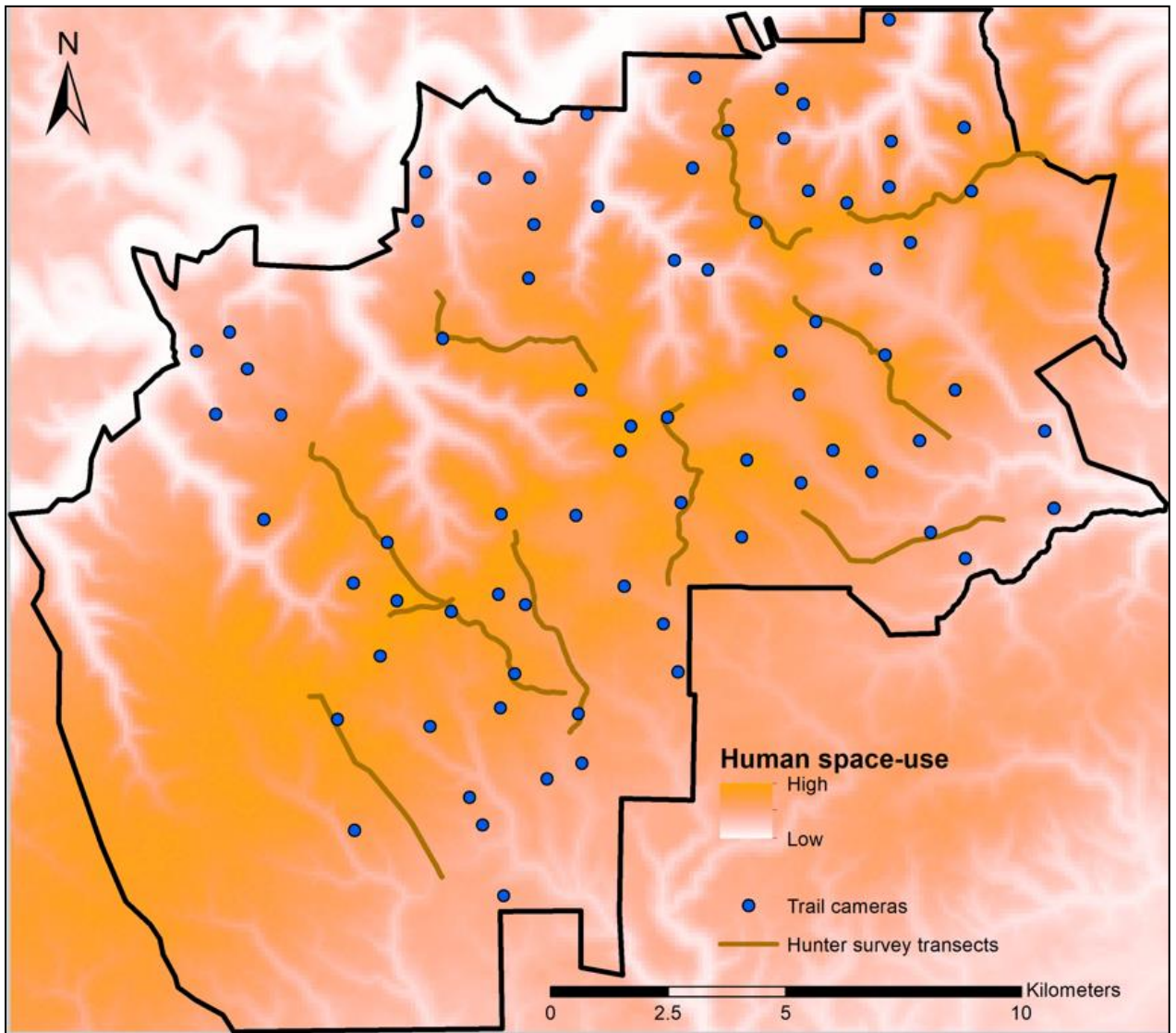


Figure 2.2. Camera locations (2020–2021), hunter survey transect locations (2019–2021), and human space use during fall (2019–2021) in the Sproul State Forest in northcentral Pennsylvania.

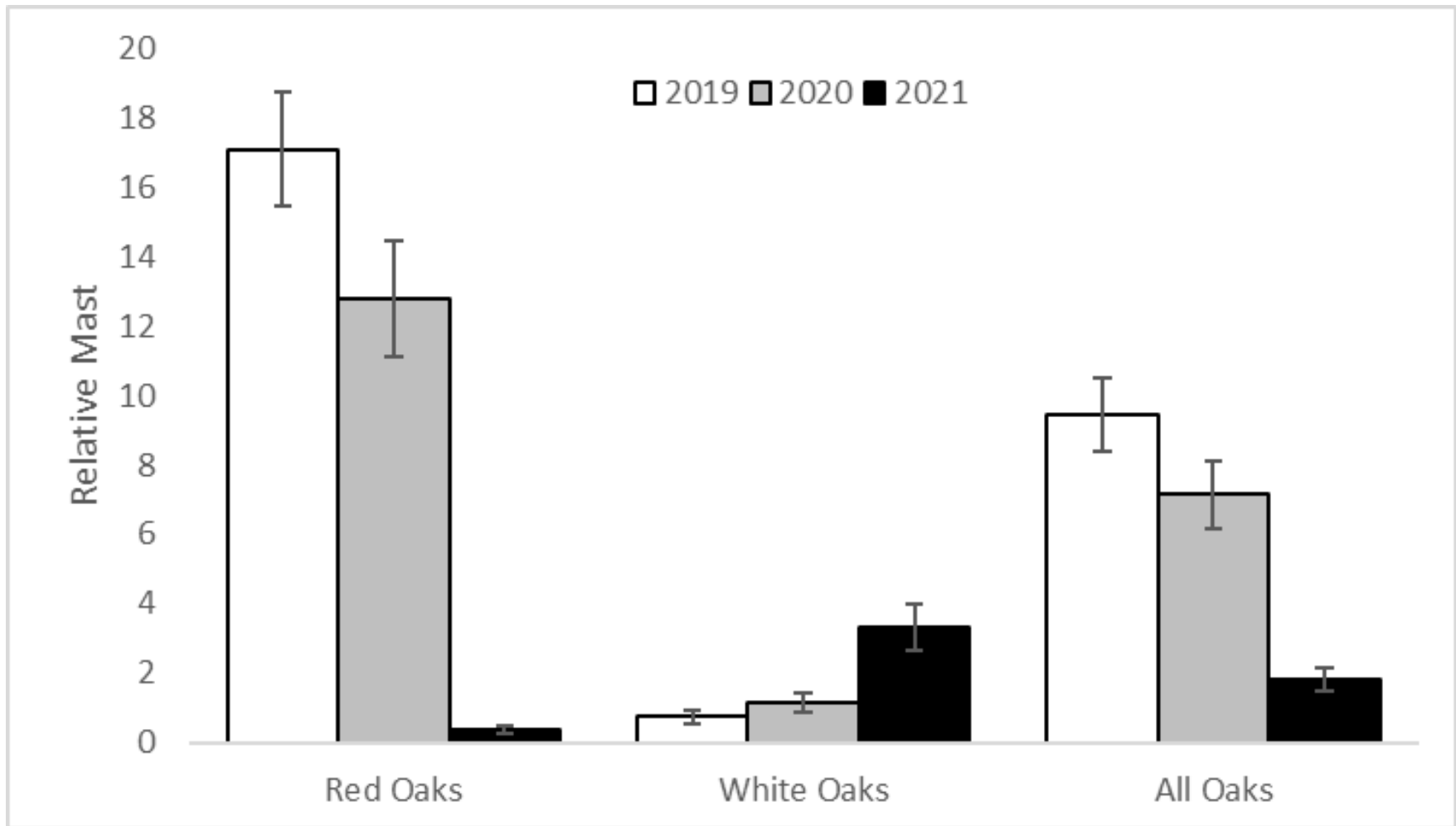


Figure 2.3. Relative hard mast production mean estimates and 95% confidence intervals for red oak, white oak, and all oaks (combination of all sampled trees) on the Sproul State Forest in Northcentral Pennsylvania from 2019–2021.

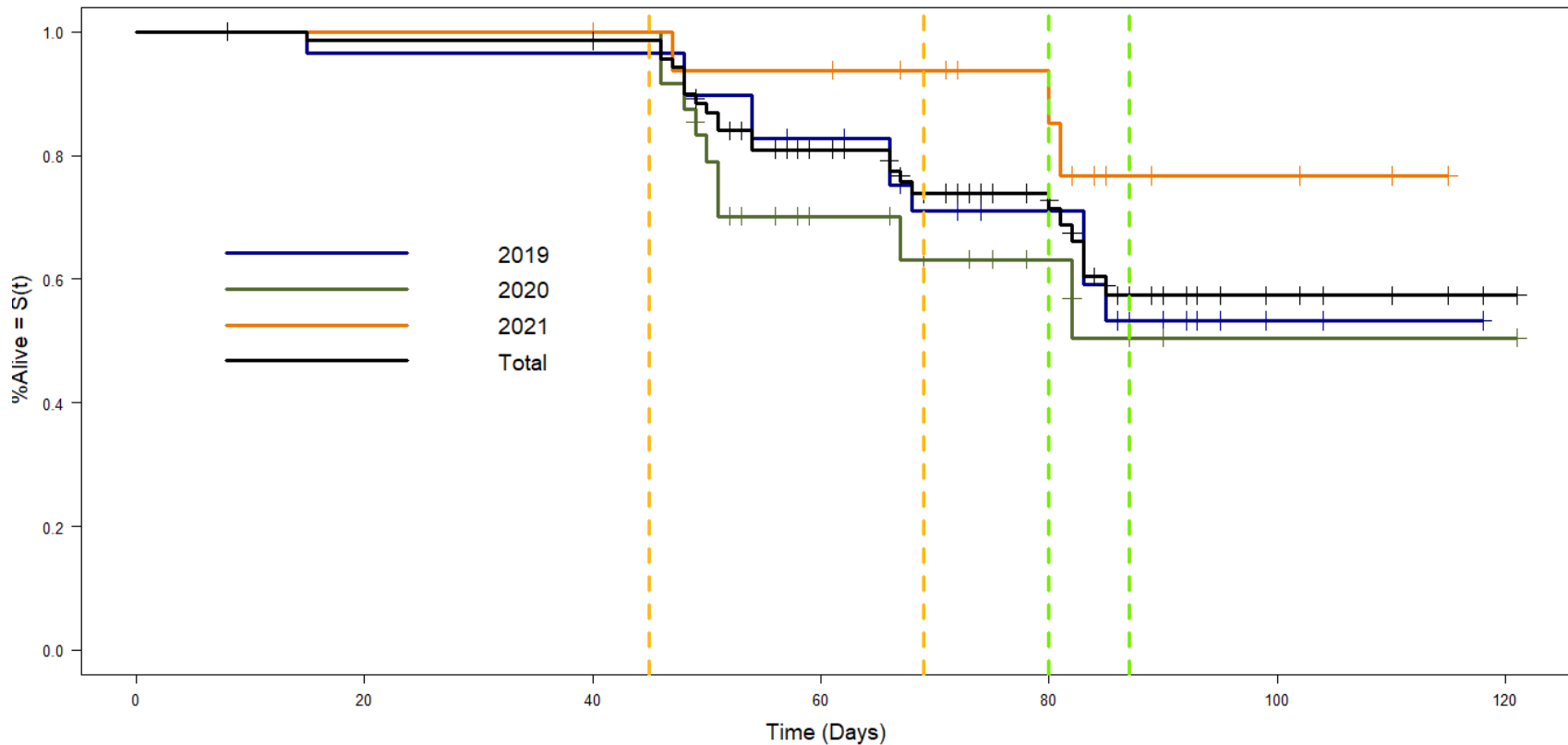


Figure 2.4. Kaplan-Meier estimates of survivorship between September 1 and mortality events, den entry, and collar malfunctions for radio-collared adult female black bears (*Ursus americanus*; $n = 29$ in 2019, $n = 24$ in 2020, $n = 18$ in 2021, $n = 71$ in total combined years) in the Sproul State Forest in northcentral Pennsylvania during fall (2019–2021). Dashed vertical lines demarcate earliest and latest timing of seasons (orange = muzzleloader, archery, and special firearms seasons, green = general firearms season).

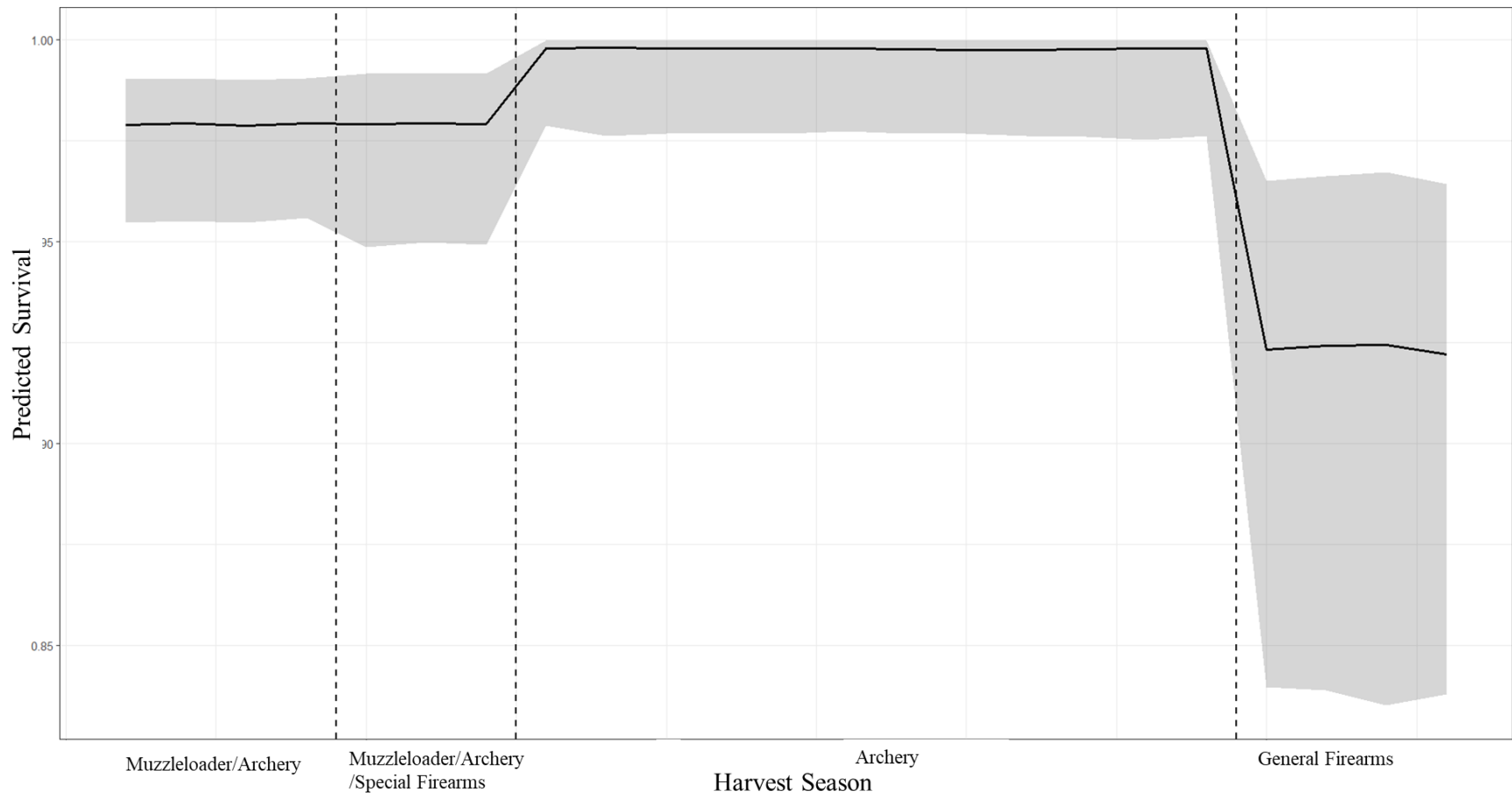


Figure 2.5. Daily probability of survival of GPS-collared adult female American black bears (*Ursus americanus*) during fall (2019–2021) bear harvest seasons in the Sproul State Forest in northcentral Pennsylvania. Note: dashed lines indicate harvest season change; periods not open to harvest were excluded from analysis.

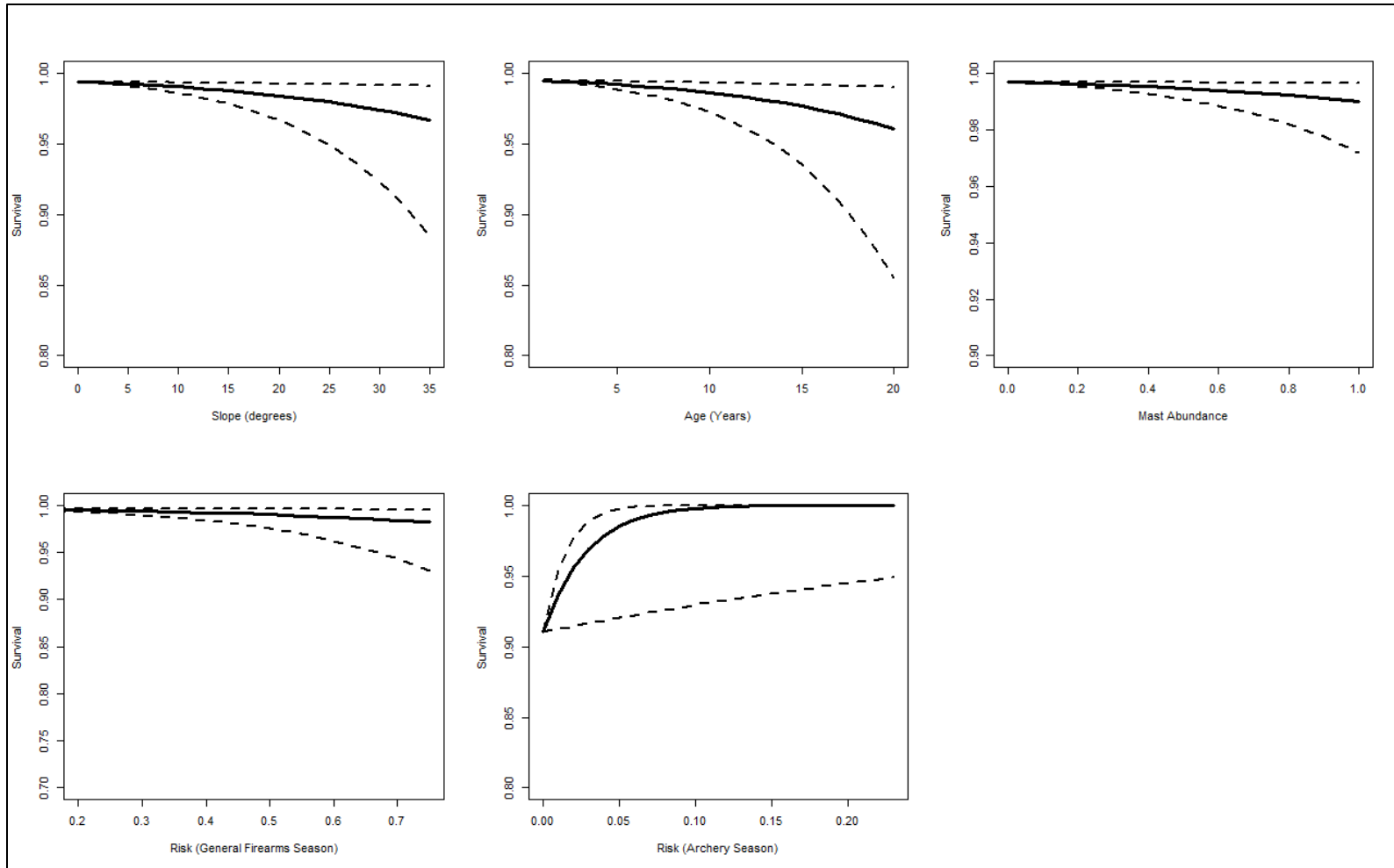


Figure 2.6. Probability of survival of select covariates from the most-parsimonious known-fate model for GPS-collared adult female American black bears (*Ursus americanus*) during fall (2019–2021) bear harvest seasons in the Sproul State Forest in northcentral Pennsylvania. Illustrations are representative of mean covariate estimates and abundant mast years (1), outside of their respective figures.

APPENDICES

APPENDIX A. List of *a priori* models used to assess weekly third-order resource selection of adult female black bears (*Ursus americanus*) in the Sproul State Forest in northcentral Pennsylvania during fall (2019–2021).

Model #	# of Parameters	Covariates
1	1	Null model
2	9	Global Model (Slope+Elevation+Stream+Camp+Oak+Paved+Secondary+Tree Height)
3	2	Slope
4	2	Elevation
5	2	Stream
6	2	Camp
7	2	Oak
8	2	Paved
9	2	Secondary
10	2	Tree Height
11	3	Paved+Secondary
12	3	Slope+Elevation
13	4	Camp+Paved+Backroad
14	4	Slope+Elevation+Stream
15	6	Slope+Elevation+Stream+Oak+Tree Height
16	3	Oak+Tree Height
17	4	Oak*Tree Height
18	3	Stream+Oak
19	3	Slope+Oak
20	3	Slope+Tree Height
21	4	Slope+Tree Height+Secondary
22	4	Slope+Oak+Tree Height
23	3	Slope+Stream
24	4	Slope+Stream+Tree Height
25	5	Slope+Stream+Tree Height+Paved+Secondary
26	5	Slope+Stream+Tree Height+Paved
27	5	Slope+Stream+Tree Height+Secondary

VITA

Brandon Michael Snavelly

Candidate for the Degree of

Master of Science

Thesis: HOME RANGES, RESOURCE SELECTION, AND SURVIVAL OF ADULT FEMALE BLACK BEARS IN A MIXED-OAK HABITAT TYPE IN NORTHCENTRAL PENNSYLVANIA

Major Field: Natural Resource Ecology and Management

Biographical:

Education:

Completed the requirements for the Master of Science in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, Oklahoma, USA in May, 2023.

Completed the requirements for the Bachelor of Science in Environmental Science at Paul Smith's College, Paul Smiths, New York, USA in May, 2016.

Experience:

Previously employed by the Pennsylvania Game Commission (Wildlife and Fisheries Biologist Aide; 2015–2021)

Professional Memberships:

The International Association of Bear Research and Management (IBA)

The Wildlife Society (TWS)

Ducks Unlimited (DU)